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GEORGINIDAE, NEW FAMILY OF ACTINOCERATOID CEPHALOPODS, MIDDLE ORDOVICIAN, AUSTRALIA

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ABSTRACT

150 Actinoceratoid cephalopods from Lower Middle Ordovician rocks in Toko Syncline, Georgina Basin (NW. Queensland and E. Northern Territory) have siphuncular calcification in which not only does each annulus consist of a hollow ring of enveloping wall enclosing radially arranged lamellae but a series of more massive calcareous growths are formed on the inside of the connecting rings, and engrafted across the plane of contact of adjacent annuli (the interannulus) as they and the annuli grow. Both are formed of fine calcareous spicules normal to apparent membrane surfaces. The canal systems are closely comparable with those of normal Actinoceratida. This new family Georginidae comprises *Georgina* n.gen., *G. andersonorum* n.sp., *G. taylori* n.sp., *G. beuteli* n.sp., *G. linda* n.sp., *G. dwyeri* n.sp., *Mesactoceras arachne* n. gen., n.sp. The last 3 occur in younger beds than the remainder, but only *G. beuteli* and *G. dwyeri* could evidence parts of an ancestor-descendant series.

In 1970 Mr D. J. Taylor of Sydney suggested to me that the collection and study of the Coolibah Formation nautiloids (which he had sampled in 1958) would be a rewarding project. He specified the two richest areas he had observed, one of which, Halfway Dam on Tobermory Station, was exceptional. Collecting trips made in 1971, 72, and 74 have amply justified his advice.

The Lower Palaeozoic Georgina Basin extends from NW. to SE. across the border of the Northern Territory of Australia and Queensland (Fig. 1a). To the SE., it is lost to sight beneath younger sediments of the Great Artesian Basin. Its main sediments are predominantly low dipping Cambrian and Ordovician rocks; known Silurian rocks are restricted to Toko Syncline (the most southerly major structure exposed) and known Devonian rocks to a few synclines, one of which is Toko Syncline. The subject of this paper is part of the Ordovician nautiloid fauna of Coolibah and Nora Formations in Toko Syncline. The syncline takes its name from Toko Range which is formed by the NE. limb and axial plateau north of the fault zones near Burnt Well, Tobermory (Fig. 1c). Toomba Range is the SW. limb of the syncline. The scarps of the ranges are formed by Carlo Sandstone, conformably above Nora Formation which forms the lower part of the scarps (where it is often totally concealed by talus) and a varying width of surrounding flat land. Coolibah

Fm. embraces the ranges and may form a low secondary ridge. In Toomba Ra. extensive faulting and outwash deposits conceal it from just north of Gap Homestead to 4.8 km S. of Eurithethera Soak. At this spot (L326 on Fig. 1c) a tiny outcrop of its upper beds is sandwiched between Nora Fm. and a strike fault which brings light grey Ninmaroo Fm. limestone against similar upper Coolibah limestones. This is the only known outcrop of its upper beds in Toomba Range but the middle beds outcrop further S. because the fault is not quite parallel to the strike. Its southward extension is concealed N. of a series of en echelon transverse faults which displace the tip of Toomba Range. The presence of this unmapped strike fault may help to account for the report of a local fourfold increase in thickness of the Coolibah Fm. in this region (Reynolds 1968, an unspecified section).

Smith (1972) has summarized years of geological mapping by geologists of the Bureau of Mineral Resources, Geology and Geophysics aided, in Queensland, by the Queensland Geological Survey. The Bureau of Mineral Resources 1:500,000 geological map Georgina Basin sheet 4, compiled by Smith (1965b), was the base map used in Fig. 1c. In this map and in Smith (1972) the Lower to Middle Ordovician boundary is placed between Coolibah and Nora Fms. on unpublished palaeontologic evidence. This course was also followed in the 1:250,000 geological map series SF/54-9, 13,

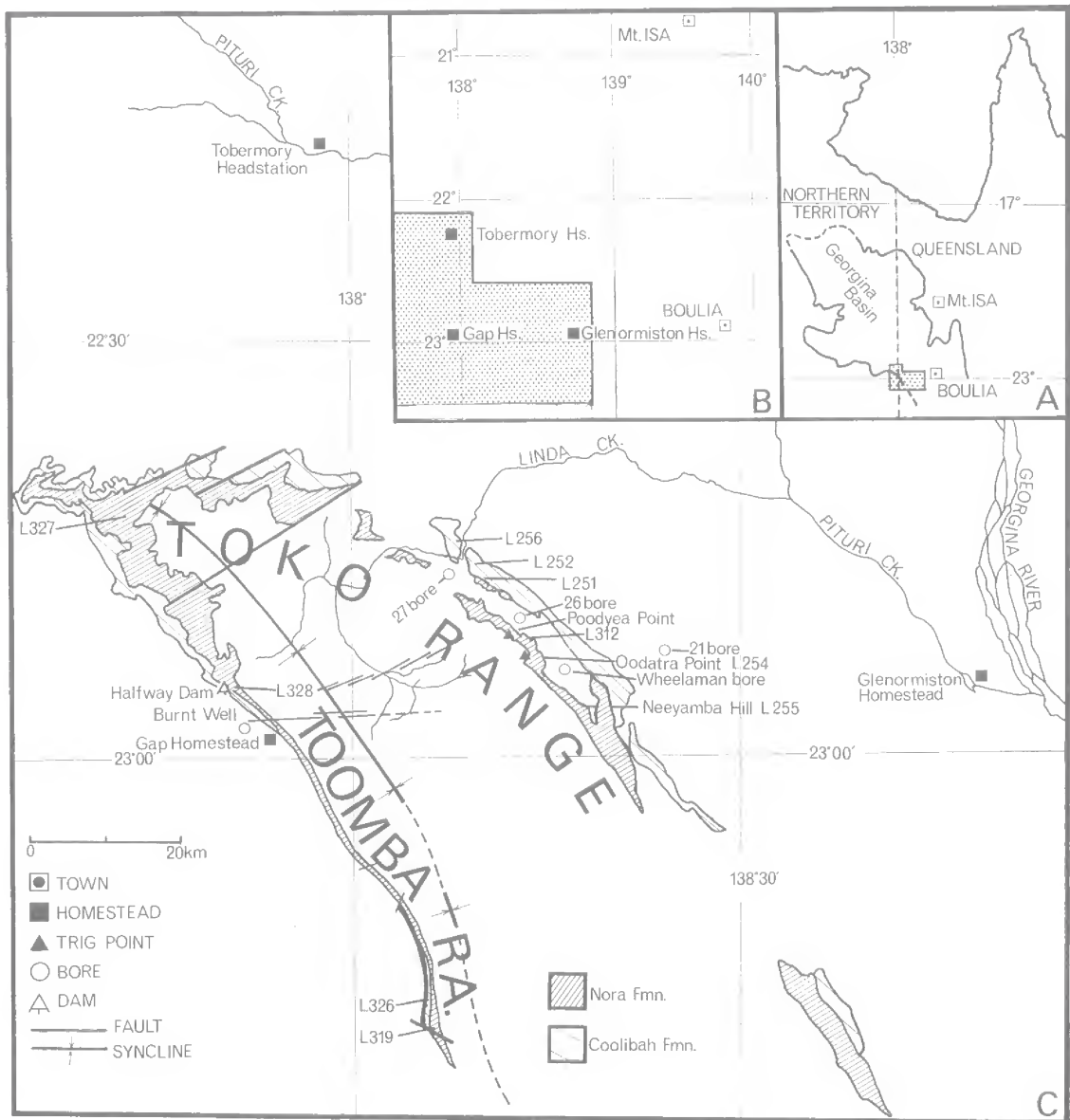


FIG. 1a-c. Locality plan of Georgina Basin and Toko Syncline showing outcrop of Coolibah and Nora Fms, Lower Middle Ordovician, embracing Toko and Toomba Ranges. After Smith, 1972.

SF/53-12, and in the explanatory notes to accompany those sheets: Glenormiston, Mt Whelan (Reynolds 1965, 1968) and Tobermory (Smith 1965a). This placing is still under mainly verbal debate by workers on several fossil groups and cannot be regarded as final. Two *Armenoceras* sp. appear among the earliest nautiloids in Coolibah Fm., about one third of its thickness above its base, and of them one is long-ranging and reaches virtu-

ally to the top of the formation, being accompanied in the last one or two metres by two larger species of *Armenoceras*. These faunas are necessarily post-Canadian and, although new species, would appear to be quite high in the Whiterock (Flower 1968, fig. 1), were it not for the accompanying endocerids which have a low Whiterock aspect (Flower, pers. comm.). The entry of large *Armenoceras* in the highest Coolibah

beds is followed, in limestone lenses in the lower third of the Nora Fm., by a much richer fauna of still larger *Armenoceras* and the first *Actinoceras*. The endocerids however have an older aspect and it seems unlikely that these beds can be considered younger than Chazy (Flower, pers. comm.), so this numerous species is the oldest known *Actinoceras*. The nautiloids figured by Hill, Playford and Woods (1969) from Nora Fm. include three specimens mistakenly published as from Coolibah Fm. (Hill, Playford and Woods 1969, pl. OII, fig. 8 and pl. OIII, figs. 6, 7); they bear the original University of Queensland locality number L271 = 'base of low mesas S. of Wheelaman Bore' besides being unsilicified like the Nora fossils and unlike any rock-free Coolibah fossils. Both species of the U.Q. L271 specimens are found in a widespread lower Nora fauna richest at L319 in

Toomba Ra., while the remainder of Hill, Playford, and Woods' figured specimens are from another widespread lower upper Nora fauna. Published localities for all the latter agree with locality numbers on the specimens. The overall aspect of the nautiloids thus suggests that the age of the Coolibah and Nora Fms. ranges through the Whiterock to reach Chazy possibly before the end of Coolibah deposition but certainly by the lower Nora Fm. Many elements drop out well before the top of the Nora but the highest beds are decalcified and their dating is not discussed here as no *Georginidae* were recognized in them.

The Coolibah Fm. has repetitive, variable lithology and cannot be divided lithologically; though it can already be subdivided on actinoceratoids the formal establishment of zones should await study of other nautiloid groups. It has no nautiloids in its

<div> <div> </div> <div>occurences on SW.limb</div> </div> <div> <div>•••••</div> <div>occurences on NE.limb</div> </div> <div>TOKO SYNCLINE GEORGININA</div>	Georgina taylori	Georgina andersonorum	Georgina beuteli	Georgina sp.	Georgina linda	Mesactoceras arachne	Georgina dwyeri
Upper Nora							•••••
Middle Nora							
Lower Nora							••
Upper Coolibah	 ••••• •?	 ••••• •?	 ••••• •?				
Middle Coolibah							

FIG. 2. Stratigraphic distribution of *Georginidae* in the Middle Ordovician of Georgina Basin.

basal part, a fauna of endoceratoids, *Armenoceras* spp. discosorids, and a tarphycerid from one third of the way above the base, and an upper fauna which includes further species of *Armenoceras* and the new actinoceratoids described below as the new family Georginidae. On the NE. limb the lower fauna is the better developed while the upper fauna is the better on the SW. limb. The Georginidae enter at approximately the same level (Fig. 2). Also shown on this chart is a discontinuous series of occurrences in the conformably overlying Nora Fm.

The Nora Fm. is lithologically variable between sandstone and coquinite; when fresh it is strongly glauconitic, and phosphate nodules occur intermittently. Thicknesses vary greatly (Smith 1972) as does the proportion of carbonate. Nautiloids are confined to the beds with carbonate (or clearly decalcified beds now sandstone, forming the top of the formation). Georginidae occur in lenticular carbonates at three levels in the Nora. There is a supporting fauna of other nautiloids so that the sequence of forms shown in Fig. 2 is considered reliable even though large-scale lensing of beds makes nonsense of lithological subdivision without very detailed fieldwork. Reynolds (1965) discussed the Nora Fm. in terms of a 'basal' portion of fine sandstone to coquinites 120 feet [36 m] thick, and an overlying sequence of siltstone to sandstone 76 feet [23 m] thick. Abundant moulds in many layers testify to a laterally variable, high proportion of shell carbonate originally having been present in this upper portion. Nautiloid internal moulds are of endoceratoids and possible discosorids and actinoceratoids but no Georginidae are known. Generally in the syncline, these highest beds are somewhat transitional to the overlying Carlo Sandstone. Of the three divisions in Fig. 2, lower, middle, and the lower part of the upper division are all equivalent to Reynolds' 'basal' 120 feet [36 m], the blank upper part of the upper division is equivalent to Reynolds' 76 feet [23 m] siltstone to sandstone. This usage is based on the sequence at L319 on the E. side of Toomba Ra. scarp (where the base is concealed). There a large lens, estimated to be about 1/3 of the distance from bottom to top of the formation, contains the rich 'lower Nora' fauna (including 3 georginids, one undescribed because all specimens are worn). This fauna is known elsewhere from lenses at L251 near the observed base of the formation, and L327 (Fig. 1). At about 2/3 the distance from bottom to top of the formation near L319 a thin lens of limestone carries the 'middle Nora' fauna, endoceratoids and one of the three georginids (*Mesaktoceras*; a thicker lens in this position near Halfway Dam also

contains this georginid). An upper bed, not far below the sandy beds that grade into the overlying Carlo Sandstone, contains the fauna which accompanies the largest georginid known (as yet found only on the NE. limb), the 'lower upper Nora' fauna. This georginid occurs in the lower half of a major coquinite near the top of Reynolds' 'basal' bed. On the NE. limb the lower fauna is known only from an old collection of F. W. Whitehouse (Univ. Qd L271) and Qd Museum L251. The section is thinner, and phosphatic nodules are very generally larger and more common than on the SW. limb. Attenuation appears more likely to be due to repeated reworking than to a major disconformity; frequently specimens have been planed off after burial and later re-buried by sediment. Some have been planed off more than once.

DEPOSITORIES

Most holotype and paratype material is deposited at the Queensland Museum, register numbers F7090 to F7212, F7219 to F7221. The remainder of the material is deposited at the Geology Department, University of Queensland, register nos. F66033, F60014 and F67153, and Bureau of Mineral Resources, Geology and Geophysics, Canberra, A.C.T., register no. CPC16908.

SYSTEMATICS

MORPHOLOGY OF THE GEORGINIDAE

The new family Georginidae had orthoconic shells with relatively long chambers. Only two partial phragmacones have been collected and both are of thin-walled shells without cameral deposits, though enclosing fully developed, calcified siphuncles. There are no other indications of cameral deposits. The destruction of shells speaks for their delicacy, as does the fact that septal necks and adjacent pieces of septa are very fragile for the sizes of shells indicated by the siphuncle fillings. Most of the specific descriptions are necessarily based on the siphuncular deposits which consist, as in other Actinoceratida, of calcified annuli extending from the septal necks outward along the connecting ring until they impinge on the annuli anteriorly and posteriorly, and inwards to surround an *axial space* a little larger than the axial canals. The *interannuli* (the contact areas, or zones, between adjacent annuli) are not necessarily flat but have a characteristic range of shapes in any species, frequently becoming anteriorly projected near the centre as the individual matures and septa become more closely spaced. Plate 1, fig. 5 shows the only

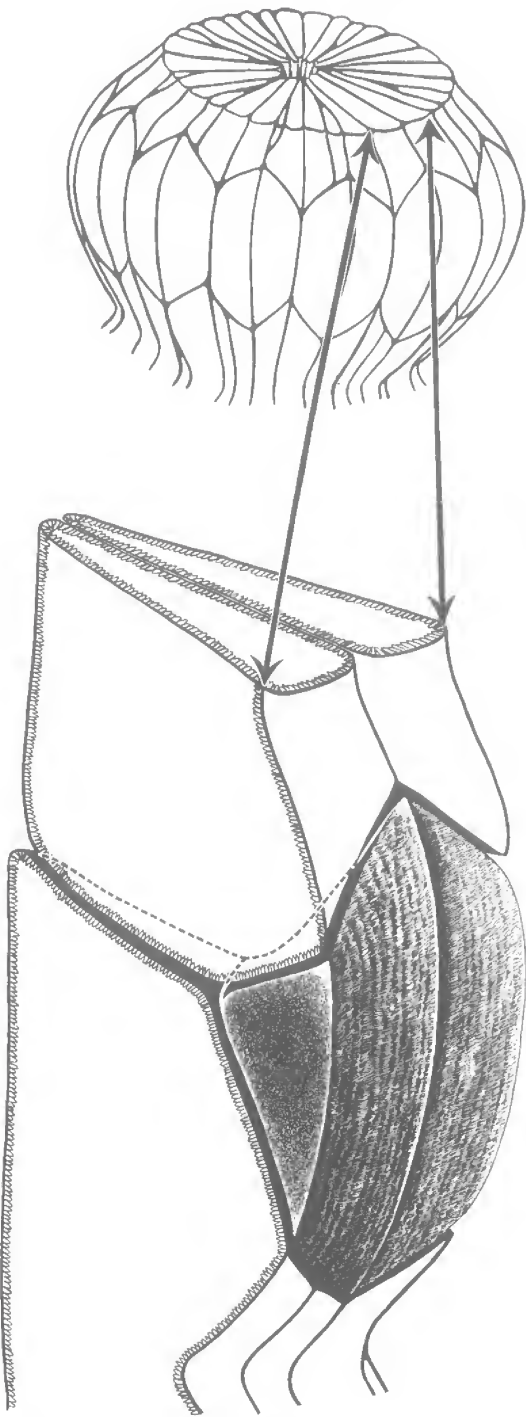


FIG. 3. *Georgina taylori* n. gen., n. sp. approx. $\times 2$ and $\times 6$. Diagram showing relation of annulus calcification normal to its basal membranes (wall membranes and radial lamellar membranes); double-walled nature of interannulus (heavy black line) and insertion of engrafts between the edges of adjacent annuli.

remains which indicate shell shape, in oblique longitudinal section.

The lack of cameral deposits is unusual in Actinoceratida but typical of Georginidae which are most obviously characterized by siphuncular deposits in which the annulus calcification is in the form of *radial lamellae* separated by spaces and enclosed within the hollow walls of each annulus (Fig. 3). The calcified radial lamellae and annulus walls are built by growth of fine, small crystals elongated normal to membrane surfaces, both *lamellar core membranes* and *annulus wall membranes*. More significantly, Georginidae have an additional series of calcifications engrafted across the outer edges of each interannulus (Figs. 3–5). These structures are here termed *engrafts* as they are inserted into, and incorporated in, adjacent annuli and join them together. The engrafts originate as calcification around longitudinal membraneous ridges on the insides of connecting rings, the *engraft core membranes* which divide perispacia into longitudinal *perispacial sinuses*, as distinct from those of normal actinoceratoids. A system of axial and radial canals and *segmental sinuses* adds to their actinoceratoid resemblances. The lamellar structure is less distinct from the contrasting massive calcification of the normal actinoceratoids than would appear from many actinoceratoid texts. Wade (MS) shows that similar calcification normal to radial lamellar membrane surfaces is characteristic of Actinoceratida in general, although frequently lamellar calcification is of crystals long enough to abut between adjacent lamellae, so that no empty spaces are left between lamellae and recrystallization is facilitated. Teichert and Crick (1974, pl. 2, fig. 3 in particular)

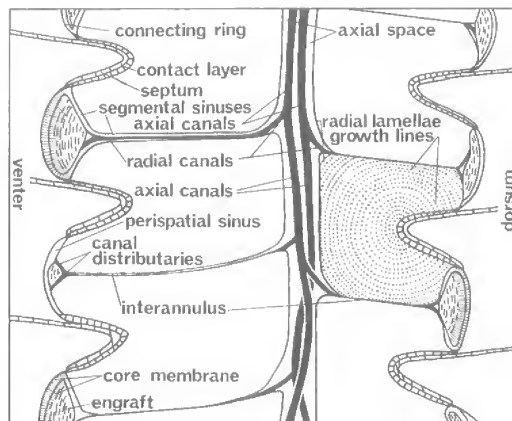


FIG. 4. *Georgina taylori* n. gen., n. sp. approx. $\times 4$. Sagittal section showing canals (axial and radial) and sinuses (segmental).

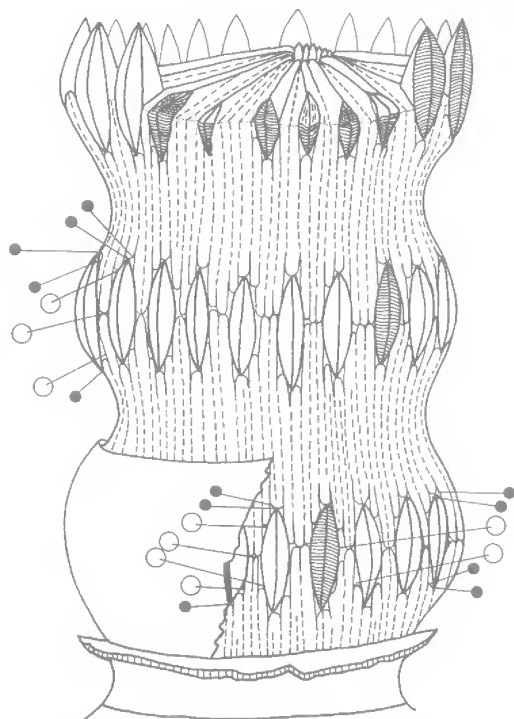


FIG. 5. *Georgina andersonorum* n. gen., n. sp., approx. $\times 2$. White-headed pins: openings of radial canal distributaries. Black-headed pins: openings of segmental sinuses. Upper surface shows an interannulus and views of engrafts.

have figured a normal actinoceratid with similar short lamellar calcification, *Huroniella severnense* (Foerste and Savage); in this specimen the interlamellar space was partly filled and partly empty. The empty portion they considered a perispatium, equating the annulus wall with the connecting ring, and thus describing the radial lamellae as growing in from the connecting ring (i.e. like engraft core membranes). Small fragments of the actual, very thin, connecting ring are seen in their pl. 3, figs. 2, 5?, where they cover the grooves in the annulus wall that mark the position of the radial lamellae (compare Figs. 3, 5 in this paper). *H. severnense* has convergently short lamellar calcification, but is otherwise as distinct from the much older Georginidae as any other Actinoceratida. Teichert and Crick (1974) gave a short review of literature in which radial lamellae have been described in the past. These are much less numerous than papers in which they have been figured. Similar structures have been observed in other Actinoceratida including *Nybyoceras multicubiculatum* Teichert and Glenister (1953, p. 203), *Wutinoceras logani* Flower and *W. lobiferum*

Flower (1968) and numerous other authors' illustrations. The radial membranes are much stronger in the Georginidae than in *Armenoceras* from the same beds, but no stronger than those in a superb *Kochoceras tyrelli* from Red River limestone, Garson Mine, near Winnipeg, Manitoba, loaned by Flower. This shows radial lamellae of rather chalky calcite on each side of lamellar core membranes, separated from neighbouring lamellae by clear, crystalline calcite.

The septal necks of the two most common Coolibah Fm. species are extremely varied; their range is from suborthochoanitic to recumbent cyrtchoanitic. By Nora Fm. time the shape of the neck was stabilized early in individual growth in every species.

The simplest form of siphuncle calcification displayed by Georginidae is illustrated in Fig. 5, *G. andersonorum*. Only young growth stages are suborthochoanitic, later stages in the same species become cyrtchoanitic. Certain similar, slightly inflated, young stages are without engrafts and not now assigned. There is little difference between those with very small or no engrafts. The latter could be extremes of variation in *G. andersonorum* or the young stage of certain adult specimens which have been rolled to cylindrical shape. Nothing is known of their phragmocones except the chamber spacing which can be inferred. There is no trace of septal necks nor connecting rings, so not even the possession of perispatial sinuses is provable. Their radial canals lie in interannuli which are flat to slightly convex, and, taken in conjunction with the axial space, growth lines and general proportions, make up a generally georginid plan. The stratigraphically oldest individual is a small specimen of this kind from the lowest Coolibah nautiloid fauna at L256, 1/3 of the thickness above the base. It seems possible that this is a poorly known relict ancestral form that may be more sensibly described later under its own familial name, so no attempt is made to define the family Georginidae broadly enough to include these specimens.

The Georginidae are distinguished from all previously described actinoceratoid families by the possession of engrafts. These include both *engraft core membranes* which grow in from the connecting rings and divided each perispatium into a series of longitudinal perispatial sinuses, and *engraft calcification* of fibrous crystals which added many growth lines during their increase in length, finally ceasing growth when the developing annuli engrafted them into their outer edges across the interannuli. The differences between the sets of associated structures in georginid and other actinoceratid siphuncles are

ERRATUM

Page 7, Column 1, 17 lines from bottom should read:
connecting rings, and is incorporated in the outer



so basic as to suggest that they pre-dated calcification of both groups of siphuncles. Another major difference is that georginids appear to have totally lacked cameral deposits while other actinoceratids normally possessed them adapically. This also suggests early separation of normal Actinoceratida and Georginidae. On the other hand the resemblances are even more far-reaching when all nautiloids are considered.

Species are differentiated largely on the shapes (or ranges of shapes) of septal necks and annuli, the approximate position of the neck within a septum (as indicated by the angle between neck and axis) and differences of proportion. A genetic level of diversity is recognized for a rather late species which is divergent from all others in having reduced annuli and a series of irregular endocones which constrict the functional size of the axial cavity to the approximate proportions of the cavity enclosed by the annuli of the other species. Accordingly, the strongly lamellar actinoceratoids with engrafts are here classified as family Georginidae, genera *Georgina*, *Mesactoceras*.

FAMILY GEORGINIDAE n. fam.
Figs. 3-7

TYPE GENUS: *Georgina* n. gen.

DIAGNOSIS: Fragile, longiconic orthocones with suborthchoanitic to recumbent cyrtchoanitic septal necks, sometimes with a strong contact layer; connecting rings thin, inflated. Siphuncular calcification of vertical radial lamellae within a hollow ring formed by the annulus walls, both lamellae and walls consisting of minute, elongate, calcareous crystals normal to radial membranes and to the insides of annulus wall membranes, and also a series of massive engrafts which radiate inward from longitudinal puckers of the insides of the connecting rings thin, inflated. Siphuncular calcified edges of the annules, bridging the interannulus and diverting some to most of the radial canals. Radial canals usually break into distributaries inward from the engrafts. Canal distributaries may occur even when the engrafts are few. The radial canal system occupies the radially fluted interannuli which can be generally flat to arched, or produced anteriorly around the centre. The radial canals are consequently straight to sloped posteriad and often show some dendroid branching. Where known, the perispata consist of a series of longitudinal, strip-shaped perispatal sinuses. These are in a position to have received the distributaries of the axial canals; in addition they sometimes can be seen to connect to the axial cavities through passages (segmental sinuses) which open on the annulus

surface both before and after the septal necks. More than one axial canal is usual. The axial space enclosed by the siphuncle calcification is more or less dorsal and usually considerably larger than the axial canals. Often sloping neck-furrows indicate sub-ventral siphuncles.

REMARKS: The variety of septal necks in the earlier Georginidae indicates a pool of genetic variation which was quickly lost. The perispatal sinuses are functionally like the open perispata of other Actinoceratida and could have been derived from, or simplified into, such an open structure. The engrafts are a newly described structure, and one that gave permanency to the system of perispatal sinuses, though in forms where the engrafts are short there is no proof that perispatal sinuses did not communicate laterally at anterior and posterior. The annular calcification, coupled with axial canals, restriction of radial canals to an interannular position, perispatal sinuses within a thin connecting ring, and apparent sinuses forming return passages to the central cavity, are decidedly actinoceratoid in plan. They, and the cyrtchoanitic necks, deny the similarity of cross-sections of Georginidae and Intejocerida which have radial vertical plates continuous from segment to segment, allowing a dispersed circulatory system, without perispata.

Genus *Georgina* n. gen.

TYPE SPECIES: *Georgina taylori* n. sp.

DIAGNOSIS: Moderate-sized to large orthocones (known from siphuncles, adjacent fragments of septa, and portions of two phragmocones). Siphuncles probably all more or less sub-ventral. Necks apparently suborthchoanitic in early stages of one species, otherwise moderately cyrtchoanitic (and frequently becoming more cyrtchoanitic during ontogeny) to recumbent. Segments higher than wide to over 5 times wider than high, proportions change markedly during ontogeny of earlier species as length does not increase as much as width, and may decrease; non-adnate to adnate. Engrafts may be few and large to many and regular, varying in and between individuals. The number of radial lamellae calcified is also extremely variable. Interannuli often anteriorly convex near the centre in late stages of growth. Without appreciable extra-annular calcareous deposits in the axial cavity.

REMARKS: The canal and sinus system is illustrated by a diagram of the type species in longitudinal section (Fig. 4). In forms with strongly recurved necks the sinuses may lead within radial lamellae (Plate 4, fig. 3), rather than across the interannulus (Plate 4, fig. 7).

***Georgina andersonorum* n. sp.**
Figs. 5, 6d-f; Plate 1, figs. 1-4,
Plate 2, figs. 1-6

MATERIAL: 16 partial siphuncle fillings ranging from few to 17 segments long. All are from the upper third of the Coolibah Fm.

HOLOTYPE: F7159, from near the top of the Coolibah Fm. in the vicinity of Halfway Dam, Tobermory Station, Northern Territory. This specimen shows the full range of development of the septal necks. It was not broken or badly eroded but it has an aberrantly small amount of calcification in the last annulus.

DIAGNOSIS: Siphuncular segments large, non-adnate throughout or until strongly cyrtchoanitic necks are formed; septal necks suborthochoanitic in young stages or throughout but can quickly change to cyrtchoanitic during ontogeny; engrafts sparse to close-packed; radial canals straight to posteriorly sloped depending on whether the interannulus is near flat or anteriorly convex. Early growth lines in lamellae and anterior growth stages show that annulus calcification is at first concentrated adapically, but usually becomes symmetric about the neck.

DESCRIPTION: The species is large, only slightly smaller than *G. taylori*. It includes specimens with great individual variability in the curvature of the septal necks (Plate 2, figs. 1-3). While only large diameter specimens have strongly cyrtchoanitic late chambers, and at the last the character is introduced rapidly, some of the longest have not reached this stage at all (Figs. 6d-f; Plate 1, fig. 4). Whether every adult in the species would have reached it is uncertain but the trend to sharper inter-segmental constriction is generally present.

The anterior cavity usually grades in through a number of segments but in the holotype at least one third of the diameter of the interannulus is exposed about the centre of the last half-annulus so that radial canal furrows show in the interannulus. At one side the upper half-annulus is broken away and the whole length of the furrows is seen. Study of this area shows that the engrafts also were atypically developed in this area and confined below the interannulus. Concentration of the early calcification below the septum during growth of the annuli is common in the species.

Where engrafts are broad, the sinus openings appear more numerous than one pair each side of the engraft core at the tips of each calcification (Plate 2, figs. 1, 3).

REMARKS: Comparisons of this species with *G. taylori* and *G. beuteli* are found under those species.

The species is named after the Anderson family, owners of Tobermory Station, whose many kindnesses greatly assisted field work.

***Georgina taylori* n. sp.**

Figs. 3, 4, 6h-p; Plate 2, fig. 7; Plate 3, figs. 1-6;
Plate 4, fig. 1

MATERIAL: About 70 partial siphuncle fillings ranging from 1-18 segments in length, and to 4.42 cm in maximum known width. All are from the upper third of the Coolibah Fm. This level is much richer on the SW. limb of the syncline than the NE. but usually concealed in both areas.

HOLOTYPE: F7148, from near the top of Coolibah Fm. in the vicinity of Halfway Dam, Tobermory Station.

DIAGNOSIS: Large, relatively long-chambered shells (dimensions of phragmocone unknown, length of calcified siphuncle estimated to have reached about 50 cm). Septal necks mildly cyrtchoanitic in small diameter specimens, to recumbent in larger individuals. Segments initially globular, height may increase in the early stages but tends to decrease throughout life; width increases steadily (except in some large specimens where it may slightly diminish over the last few chambers). Early segments almost normal to axis but later, wider segments tend to become oblique. Contact layer forms a platform in the intersegmental constriction. In addition to radial canals (presumably arterial) a series of openings at the upper and lower ends of engrafts lead into sinuses in the interannulus or oblique canals within lamellae in larger specimens. (These seem to have been a venous system running inward from the perispatial sinuses into which radial canal distributaries appear to have opened.)

DESCRIPTION: The remaining shell fragments permit the observations that the septa were extremely thin for the chamber height, and that there is no evidence of cameral deposits. The septal necks are sometimes thickened relative to the septa, particularly if they are recumbent. The necks are fully lined by connecting ring material; this is so at all stages of growth. The neck linings form strongly calcified contact layers. On lightly etched specimens these form platforms with edges standing above the adjacent siphuncular beads, when the necks are dissolved away. A two-layer effect may be seen which comprises the contact layer and a darker layer like the remainder of the connecting ring in texture, presumably a layer containing more organic material in life. The free portions of the rings may have been very lightly calcified as they are rarely preserved and extremely thin for a

structure normally calcified by elongate spicular crystals.

The outlines of a number of pieces of different sizes are shown in Fig. 6h–p, to bring out the general growth trends. It is not certain that the initial segment has been observed but the trend in small specimens is toward globular. Most specimens have a slow decrease in segment length but in Fig. 6o the rate is practically zero. As in most nautiloids the later segments of large specimens are relatively short, and in one (Fig. 6j) the segments of the anterior end are minimally narrower than the lower portion. This narrowing has been observed on 3 or 4 other specimens but all the others are somewhat deformed, as if the incompletely calcified part was slightly plastic during burial.

In transverse sections the axial cavity is seen to be irregular. In longitudinal section, therefore, it rarely runs straight from top to bottom, and may appear to change greatly in size. When preserved, the axial canals take up only a fraction of the space in the cavity (Plate 3, fig. 1d). The angles at which the radial canals diverge from the axial cavity are controlled by the growth of the calcified annuli below and above the interannulus; they tend to lie in some of the fluted depressions that result from the growth form of annuli, and to shape them in detail. The angle at which they diverge from the axial canal itself is usually more oblique than the surface of the interannulus (Fig. 4).

Plate 4, fig. 5 shows a naturally silicified and etched section of a specimen broken through the centre of the septal neck, the point of origin for all radial lamellae. It therefore shows the maximum number of lamellae in this annulus. As inward growth continued the number of lamellae diminished and the fewer, remaining lamellae reached not only further in but further up and down, reaching to the equatorial region where they abut on the engrafts which, having started growth at about the same time, were calcified masses prior to enclosure among the outer ends of the lamellae. The central furrows of the engrafts, seen in most external views, equate with the dark line or core membrane seen as the centre of calcification in sections. In Plate 4, figs. 6, 7 the connection between the connecting ring and the core is shown. It can be found in other places in these and other specimens. The canal distributaries lead to the surface around or between the engrafts. Because the inside of the connecting ring extends inward as the cores of the engrafts (Fig. 4) the perispantium is divided into longitudinal strips (Plate 4, figs. 1, 2; Plate 6, figs. 1–3). At the anterior and posterior tip of each of the engrafts a pair of pores lead into the annulus. They are separated from one another by

the cores of the engrafts and (unless the neck is recumbent) lead into sinuses that run between the engrafts and the annulus walls to the interannuli (Fig. 4; Plate 4, fig. 7). They are often separated from the nearest distributary and radial canals by so little space that in section, unless both are present, it is not always possible to tell whether canals or sinuses are the structures in view. Oblique canals seen in recumbent-necked portions of large specimens (Plate 4, fig. 3) reach the surface at a spot coincident with these pores and appear to be an alternative development of the sinuses. In most specimens the ring of pores also marks the edge of the contact layer platform area, but in many specimens with recumbent septal necks the contact layer platform forms a shelf overhanging the pores without blocking them.

REMARKS: The closest species are *G. andersonorum* and *G. beuteli*. *G. andersonorum* as at present known is slightly smaller; it is nearly the same in the structures of its lamellae though early growth is concentrated below the neck; engrafts and canals are similar; it differs in being non-adnate until a very late stage of growth, and only slightly so, at most. It lacks a contact layer platform. Its early segments, or even most of its segments, are connected by wide, gently curved constrictions which most probably housed suborthochoanitic septal necks, a degree less curved than any *G. taylori*. *G. beuteli* is compared after its description.

In two most extreme large individuals the pattern of surface structures is modified to such an extent that these specimens can only doubtfully be assigned to *G. taylori*.

The species is named after Mr D. J. Taylor who first drew my attention to the locality and fauna.

***Georgina beuteli* n. sp.**
Figs. 6a–c; Plate 5, figs. 6, 7

MATERIAL: Three specimens are known from the upper third of the Coolibah Fm., Tobermory, and one from the top of the formation at Glenormiston.

HOLOTYPE: F7219, from the upper third of the Coolibah Fm. near Halfway Dam, Tobermory.

DIAGNOSIS: Moderate size with high chambers. A very smoothly streamlined profile to the beaded siphuncle is produced by smoothly rounded segments and moderately cyrtochoanitic necks with a thin contact layer that does not form a platform. Engrafts usually slender, some groups of them are longitudinally arcuate. Radial canals are relatively straight and their distributaries form a near-vertical fan.

DESCRIPTION: The holotype is the only relatively large specimen. Segment height as well as width increases throughout this six-segment piece (Fig. 6c; Plate 5, fig. 6). The contact layer still adheres in most of the constrictions but is too thin to form a platform. Segments are not oblique to the axis. Little more can be added to the diagnosis. The packing of the canal distributaries into near vertical planes is a consequence of the narrow engrafts rather than an independent character; it is a noticeable feature in vertical sections.

REMARKS: *G. beuteli* is distinguished from *G. taylora* by its very regular proportions, having mildly cyrtochoanitic necks and smoothly inflated chambers throughout its known length, unobtrusive contact layers, and slender engrafts which are not necessarily straight but can be arcuate in a longitudinal direction. It resembles *G. dwyeri* from the middle of the overlying Nora Fm. in segment shape, though it is very sharply differentiated from *G. dwyeri* by the fact its segments are not obliquely set, and contact layers are symmetrical. Its engrafts are also less frequently arcuate. Although *G. andersonorum* also lacks an obvious contact layer its necks vary abruptly from much less curved than those of *G. beuteli* to much more curved, and it virtually omits the shape of neck and segment which characterizes *G. beuteli*.

The species is named after Mr E. Beutel of the Queensland Museum, who rendered outstanding service during the 1972 trip.

***Georgina linda* n. sp.**

Fig. 6g; Plate 5, figs. 1–5, 8

MATERIAL: Two specimens from 3 km SE. of Linda Creek, Glenormiston Station, L251, in a limestone lens in the sandy lower beds of Nora Fm. Fragmentary specimens from the lower part of Nora Fm. at L319, Toomba Range.

HOLOTYPE: F7176, Glenormiston (L251).

DIAGNOSIS: Moderate-sized compact siphuncles, segments over twice as wide as long, with recumbent necks throughout (No other portion of phragmocone preserved). Axial region occupied by several parallel canals which give off 'straight' radial canals with longitudinal fans of distributaries. Engrafts narrow and usually wavy longitudinally.

DESCRIPTION: The holotype gradually increases in height and width of segments from its first to its fifth segment, and diminishes even more slightly over the sixth and seventh segments, the shorter topotype is of 3 slightly larger segments. The

specimens from L319 have deeply etched surfaces and most are single segments; some appear to have been less tightly recumbent than those from L251, but they are closely similar. The neck openings are little more than half the width of the segments at their equators (Fig. 6g). The segments are slightly oblique, the more adnate side being slightly advanced, so the siphuncles must have been slightly off-centre in the phragmocone. Free portions of connecting rings are absent but the ends of the perispatial sinuses are present between the intra-siphuncular deposits and the adnate portions of the connecting rings. A bundle of parallel axial canals is preserved in the holotype. Radial canals straight, branching in the outer portions of the interannuli, distributaries tend to form longitudinally spread fans between engrafts (Plate 5, fig. 3).

REMARKS: In its narrow, wavy engrafts *G. linda* resembles *G. beuteli* and more particularly *G. dwyeri*. It differs from both, however, in its strongly recumbent septal necks. Its slightly oblique intersegmental furrows show that it had a near-central siphuncle, more off-centre than *G. beuteli* and less off-centre than *G. dwyeri*.

***Georgina dwyeri* n. sp.**

Fig. 7a-f; Plate 5, fig. 2, Plate 6, figs. 1–3a–d

'Actinoceratid gen. et sp. nov'. Hill, Playford and Woods, 1969, p. 4, Plate O2, fig. 14.

MATERIAL: All specimens are from the lower upper Nora Fm. at the foot of Toko Range scarp, from Neeyamba Hill, Oodatra Point and 3 km SE. of Poodyea Point (L312). Since many of the specimens have been obtained in scattered fragments that cannot be fitted together, the number of individuals is in doubt. It was no less than thirty. The rock is a silty coquinite and the fossils in it have not been silicified but recrystallized and sometimes internally partly replaced with siderite which has mostly oxidized, obliterating structure; some are partly calcified internally. They tend to crumble with the rock under full exposure to insolation and cooling.

HOLOTYPE: University of Queensland F66033, from 3 km SE. of Poodyea Point, Glenormiston Station.

DIAGNOSIS: Some individuals reached large size (the calcified part of the siphuncle is estimated to have reached over 100 cm); siphuncle segments averaged a slow, rather uniform increase in width and length till a late growth stage. The siphuncle was near ventral as segments were oblique to the axis and less rotund on the advanced side where the posterior adnation area (i.e. posterior end of each segment) was flattened and consistently broad. Moderately cyrtochoanitic septal necks. Chambers long, with fragile septa. Engrafts mostly long and slender, wavy or straight. Axial canals probably

multiple, radial canals straight to posteriorly curved, some dendroid branching. Axial cavity rather broad and rounded at all stages of growth. Wavy longitudinal grooves occur on the surface of some large individuals (these may indicate perispatal sinuses).

DESCRIPTION: The size-range is large. Fig. 7a-f shows scale diagrams of specimens ranging from a minimum of 1.9 cm diameter and 1.2 cm long to 4.8 cm wide and 2.4 cm long. The longest specimen (Fig. 7e) consists of just over 27 segments and is 35.4 cm long. The next longest is a much larger individual, 17 segments occupy 33 cm; as Fig. 7a shows, it has relatively short segments for its diameter. The last few segments enclose part of the anterior cavity. If its angle of taper is produced until the width of the smallest specimen figured is reached, the length obtained is approximately 100 cm but even then both ends are missing. The section of the holotype, similarly produced, gives a length of 70 cm but no trace of the anterior cavity occurs in this (Plate 6, fig. 1a-d). One metre is thus a reasonable estimate of the possible length of a calcified siphuncle. The curvature of the septal necks is moderately cyrtochoanitic with a little variation. The segments are consistently oblique, and when the neck linings are preserved they form contact layer platforms with a pronounced broadening toward the anteriorly sloped side of the segment. This portion of the segment is flattened relative to the remainder of the segment outline, from contact with the septum. Restored shell outlines are suggested in Fig. 7b, the basis of restoration being the small, gently up-turned piece of septum showing in Plate 6, figs. 4-6, the contact layer platforms, and the almost unvarying siphuncle outlines. The perispatal sinuses on large specimens may or may not be quite deeply impressed (Plate 6, fig. 2) although small specimens are quite smooth. In addition to these channels, Plate 6, fig. 1, shows fine ridges along the cores of the engrafts, these are apparently the puckers of the inside the connecting ring. Radial canals tend to be straight in smaller specimens and posteriorly curved in larger individuals. The angles at which they meet the central cavity suggest they attached to several axial canals. Strongly oblique passages seen in several specimens have not been traced to their outer limits and may be the inner ends of sinuses which open adjacent to the contact layer platforms like those in Plate 6, figs. 5, 6. A few thin layers of secondary calcification line the apical end of the axial space in some specimens.

REMARKS: This is the only species beside the older *Mesaktoceras arachne* which has any second-

dary deposit in the axial cavity. It is here a very minor amount which scarcely constricts the axial space, and is not correlated with reduced annular deposits. The mildly cyrtochoanitic necks have a resemblance to *G. beuteli* but this yet older form is decidedly smaller and has segments which do not slope anteriorly on the ventral side, and do lack the skewed adnation area, i.e. its siphuncle was much more centrally placed in the phragmocone.

The species, which has been found only on Glenormiston, is named after the Manager, Mr J. Dwyer, in recognition of his great helpfulness to the field parties, and interest in the work.

Mesaktoceras n. gen.

TYPE SPECIES: *Mesaktoceras arachne* n. sp.

DIAGNOSIS: Georinidae with strongly cyrtochoanitic necks; engrafts well developed; radial lamellae very reduced, often not in contact in adjacent annuli and so not enclosing the inner ends of engrafts; a secondary calcareous deposit lines the irregular axial space with matchingly irregular endocones that almost fill its lower parts, enclosing canals and sinuses.

REMARKS: In the development of endocones *Mesaktoceras* has a superficial resemblance to the parietal deposits and endocones of several *Disco-sorida* but its primary deposits are the two series, annuli and engrafts, developed in all Georinidae. The canal and sinus systems enclosed by the calcareous deposits are also actinoceratoid, and appear to have been linked by vertical perispatal sinuses.

Mesaktoceras arachne n. sp.

Fig. 7g-j; Plate 7, figs. 1-7

MATERIAL: Eight specimens from 1 km east of Halfway Dam, Tobermory, from the middle of the Nora Fm. which is here relatively strongly calcareous. In Toomba Ra. one specimen was collected from a narrow calcareous bed among sandstones approximately at this level, and two from a large calcareous lens in the lower member. On the NE. limb only two small calcareous lenses at L251 occur in sandstone in this span, and only two fragmental specimens were found.

HOLOTYPE: F7187, from 1 km E. of Halfway Dam, L328.

DIAGNOSIS: As for genus.

DESCRIPTION: The largest specimen is 28 segments (approximately 34 cm long); it lacks both ends but not many segments from either end (Fig. 7h), and is distorted by dorsoventral compression. Septal necks are strongly cyrtochoanitic; in small

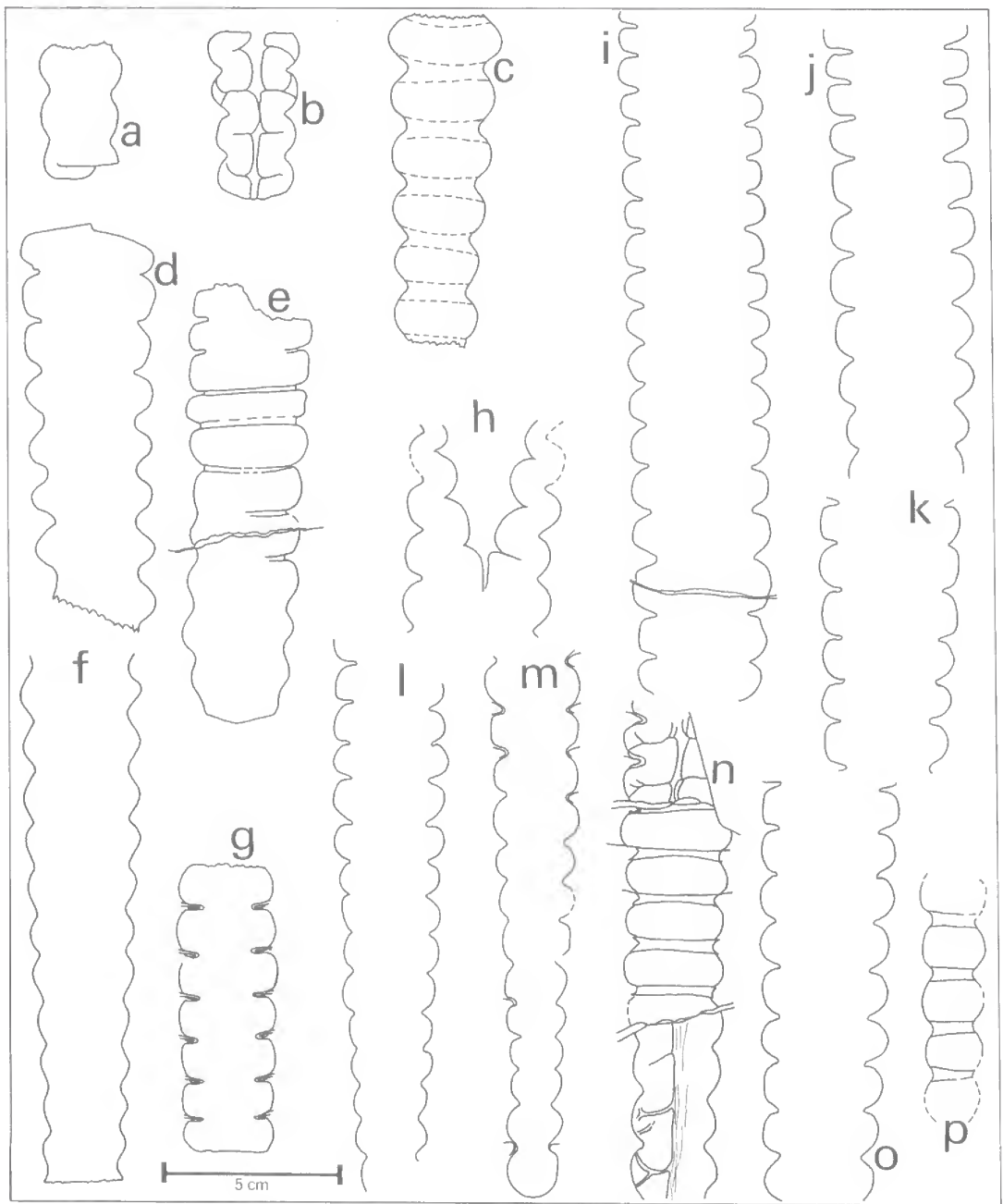


FIG. 6. Profiles of *Georgina* n. gen., $\times \frac{1}{2}$, outlines obtained by combined measuring and sketching or direct tracing off medial sections, or photographs $\times 1$. (a-c) *G. beuteli* n. sp., c = holotype. (d-f) *G. andersonorum* n. sp., d = holotype. (g) *G. linda* n. sp., holotype. (h-p) *G. taylori* n. sp., o = holotype. The initial chamber may be present on m, its anterior cavity is also present, as on h, i, and the last segment or two of other specimens.

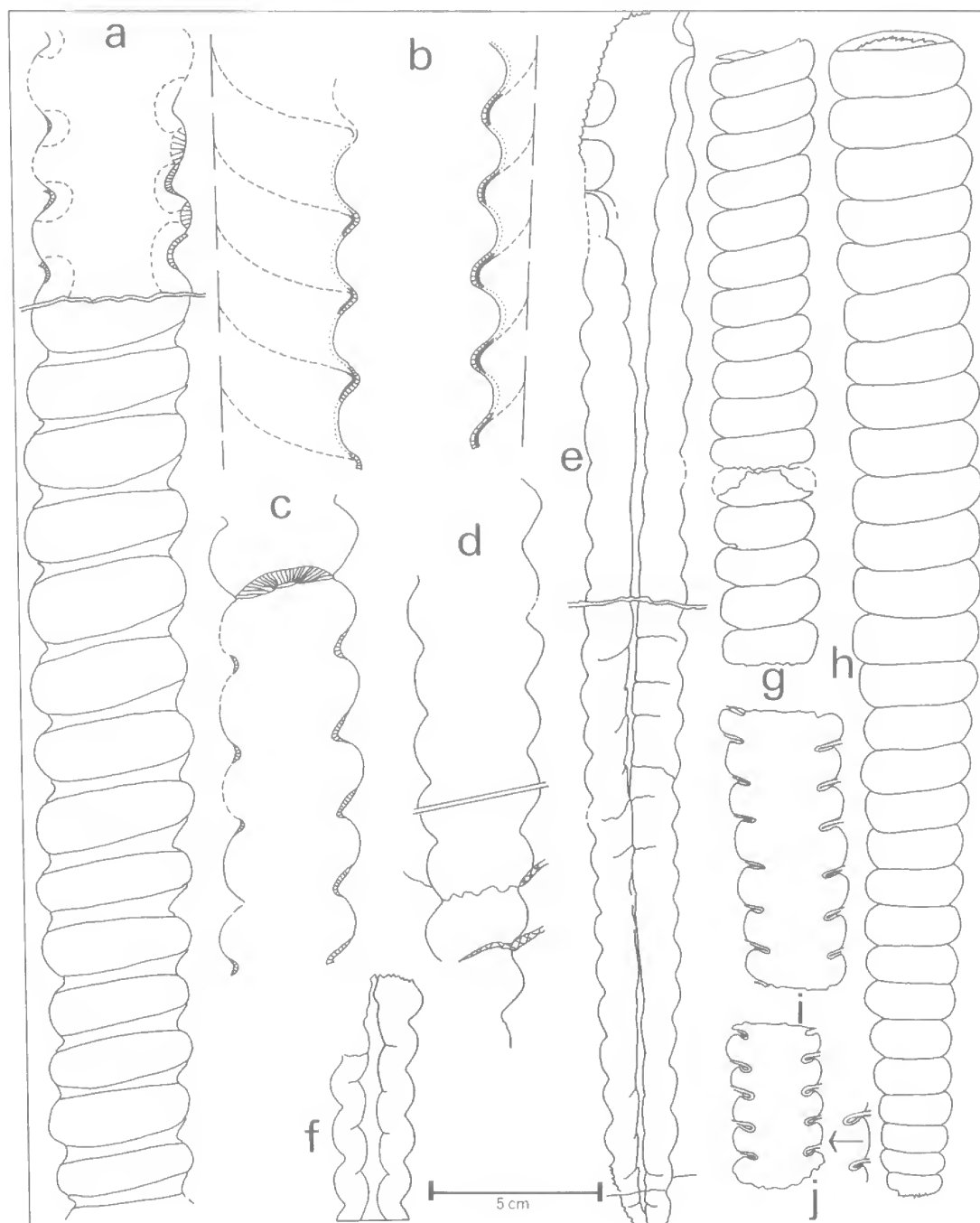


FIG. 7. Georginidae, $\times \frac{1}{2}$, profiles prepared as Fig. 6. (a-f) *Georgina dwyeri* n. gen., n. sp., b=holotype, position of siphuncle restored from adnate ventral and free dorsal edges of septum. (g-j) *Mesaktoceras arachne* n. gen., n. sp., g=holotype, h, dorsal view of longest specimen (flattened dorsoventrally, anterior cavity present but rock-filled).

specimens they have an open loop at the inner end but they become totally recumbent in larger specimens (Figs. 7i, j). The overall shape of segments changes very gradually and regularly as widening outstrips height. Contact layers are thin. The connecting rings are separated from the siphuncle calcification by a narrow gap which is now only rarely bridged by thin ridges at the cores of engrafts. This evidence is sufficient to justify the assumption that the perispantium was at least partly divided into vertical sinuses but, as in some other species, the engrafts do not always reach from septal neck to septal neck, and there is no evidence at all of whether perispantium sinuses were always complete, or fused laterally if the engraft was short.

Horizontal sections near the interannulus show only engrafts and endocones but other sections also show radial lamellae. Their size is restricted, particularly on the dorsal side (Plate 7, fig. 4). The ventral side is indicated by the anterior slope of segments as well as greater overall calcification. No canal walls are preserved but growth lines in the calcareous deposits were strongly deflected outward and appear to have encased slightly curved canals in the interannuli (Plate 7, figs. 4-6); they are usually less strongly deflected around wider spaces in the position of the sinuses (Plate 7, figs. 4, 5). It is not always possible to prove whether a particular space in an intermediate position was a canal or a sinus.

REMARKS: The classic cob-web shape of the endocones in transverse section makes even isolated segments of *M. arachne* distinct from the other known Georginidae. It is also unique in having strongly reduced radial lamellae (i.e. reduced annuli). Like *G. linda* and *G. dwyeri*, *M. arachne* is differentiated from the earlier *G. taylori* and *G. andersonorum* by much more regular shape. The slight change of its septal necks, from recumbent with an open loop at the inner end to tightly recumbent, is perceptible only in section. Although the late chambers of *M. arachne* and *G. taylori* are often similar in shape, the early to medium sizes are glaringly dissimilar (Figs. 6h-p, 7g-j). *G. linda* also is higher in proportion to width than *M. arachne*, and tightly recumbent throughout (Fig. 6g). Other named Georginidae are not recumbent.

CONCLUSIONS

The distinctiveness of Georginidae from other Actinoceratida does not rest only upon the so obvious differences in calcification which, except for the engrafts, are more a difference of degree than basic structure (Wade, MS). Cameral deposits, common in Actinoceratida, appear to have

been lacking in Georginidae. The perispantium sinuses of Georginidae do not allow secondary deposits such as have been recognized in other Actinoceratida.

One species stands apart because it alone has diminished annulus development, and it has strongly developed endocones lining its otherwise large and irregular axial cavity. Only a minute amount of secondary material lines the base of the axial cavity in any other species. This association of two well-developed independent trends has been used to separate a monotypic genus *Mesactoceras* from the remainder, genus *Georgina*. The Georginidae were successful enough to reach a large size in this shallow epicontinental sea, but their extreme fragility must have weighed against them as their size, and that of less fragile competitors, increased. The last known form, *G. dwyeri*, is the largest. Although the Georginidae at present have been found only in carbonate facies, and carbonate lessens toward the top of the Nora Fm., *G. dwyeri* ceases at a level within sandy, silty coquinities. The observed cut-out thus may be actual, and the group not succeed Lower Middle Ordovician.

ACKNOWLEDGMENTS

Besides the thanks due to Mr Taylor for drawing attention to this fascinating material, thanks are due to Dr John Jell, Mr Stan Colliver and Mr Brian Cameron who very kindly gave access to material in the collections of the Geology Department, University of Queensland. This material came from the Nora Fm. at the foot of Toko Range, on Glenormiston, (Neeyamba Hill, L271 'low mesas S. of Wheelaman Bore', and 3 km SE. of Poodyea Point) and from Toomba Range. From the earliest stages this work has benefited from the advice of Dr R. H. Flower, from his generous help with literature, and from his loan of comparative material. The encouragement and perspective gained in discussion with Dr C. Teichert have helped greatly, and he kindly read the MS. Mrs Y. Evens re-drew Fig. 3.

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PLATE I

Scales in mm.

FIGS. 1-4. *Georgina andersonorum* n. gen., n. sp., F7135, paratype, siphuncle filling only, Halfway Dam, Tobermory. 1, $\times 2$, Section through calcified material (between pointers on fig. 4) confirms shape of silicified, weathered surface and shows matrix between calcareous radial lamellae. 2-4, $\times 1$. Dorsal and anterior lateral views showing increasing relative and absolute size of engrafts and steepening curvature of septal constrictions. Broken section at right shows the lamellar annuli, interannuli, and engrafts.

FIG. 5: *Georgina* sp., CPC16908, $\times 1$. Specimen with most shell preserved. Oblique horizontal section showing a relatively small siphuncle and correspondingly low chambers.

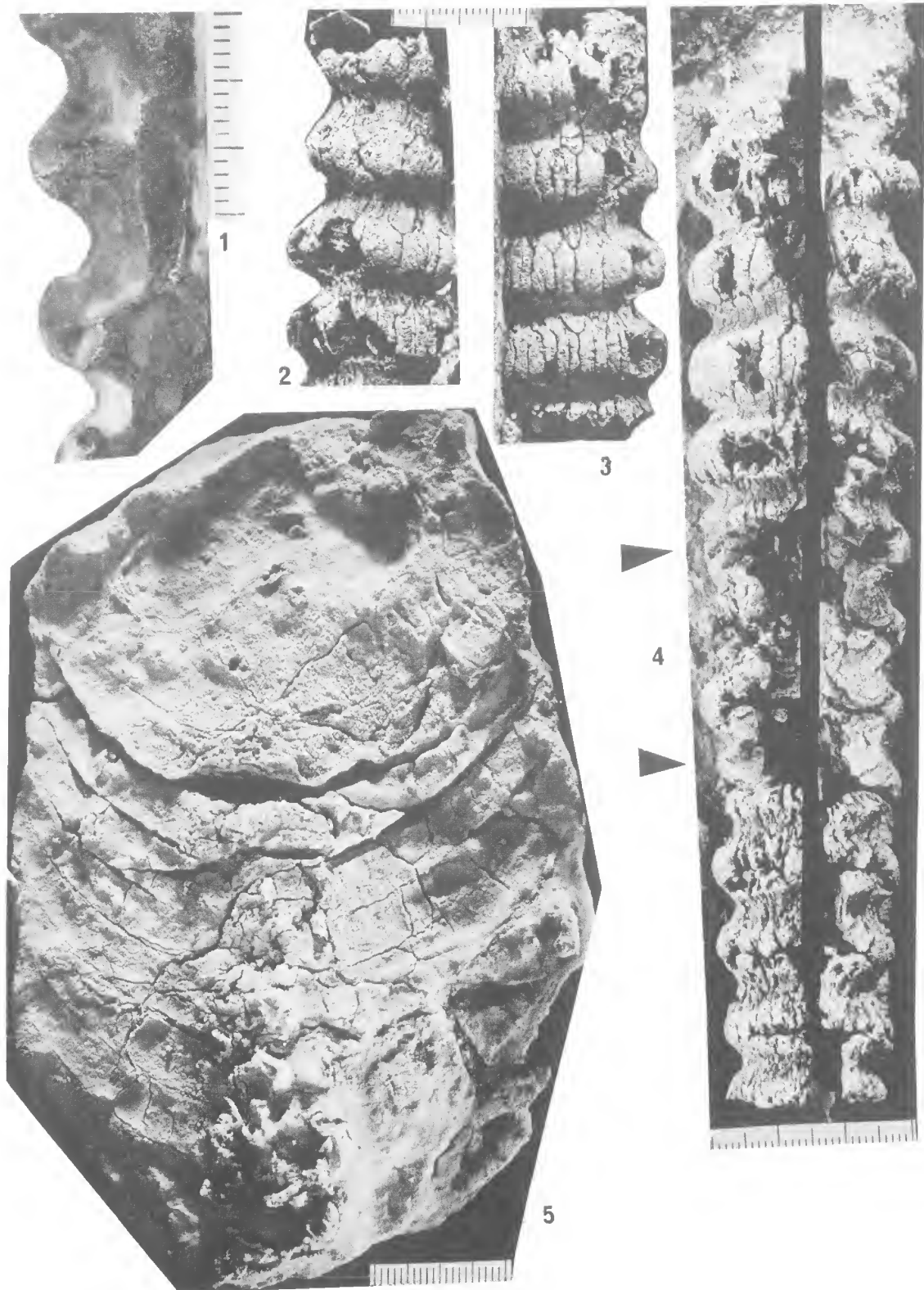


PLATE 2

Scales in mm.

FIGS. 1–6: *Georgina andersonorum* n. gen., n. sp. 1–4, F7159, holotype, $\times 1$, Halfway Dam, Tobermory. 1–3 show an abrupt transition from broadly curved to furrowed septal constrictions and predominately large, widely-spaced engrafts. 1 also shows pores (at level of pointer) that are not associated with engrafts, as well as those that are; both lead into segmental sinuses, while radial canal distributaries are nearer the bulge of the segments. 4, anterior end, shows an aberrant last half-annulus which is also broken so that the full length of radial canal furrows is exposed in the interannulus at lower right. 5, 6. F7164, paratype, 5 km. N.W. of Halfway Dam, Tobermory, $\times 2$. 5 shows 2 connecting rings and adjacent septal necks. Anterior neck bears a partly developed annulus with light grey early layers restricted to coating the posterior (free) edge. 6, posterior to 5 and opposite side of saw-cut. Anterior two segments show radial canals with one distributary each, a narrow perispantium is preserved in the anterior segment but no connecting rings are preserved in the posterior two. Segmental sinus openings occur above and below engrafts, and the Y-shaped traces of the interannular wall membranes separate engrafts from annulae.

FIG. 7: *G. taylori* n. gen., n. sp., F7134, paratype, $\times 2$. Anterior cavity in transverse section a short distance from an interannulus. Engrafts are contiguous almost all around the circumference, and are enclosed on their inner sides by blister-like sectors which together make up the part-developed annulus. Predepositional erosion has left an unnaturally rough surface.

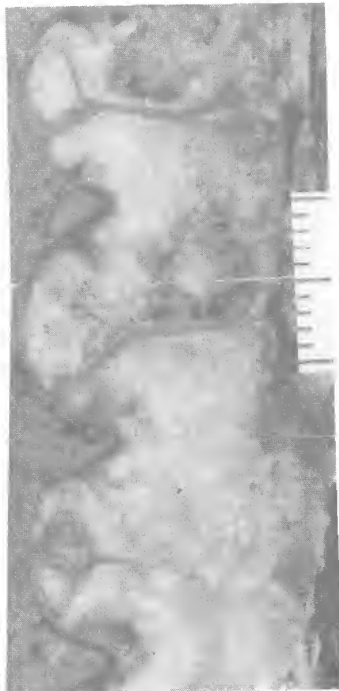
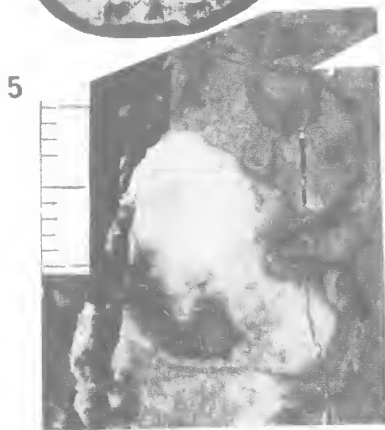
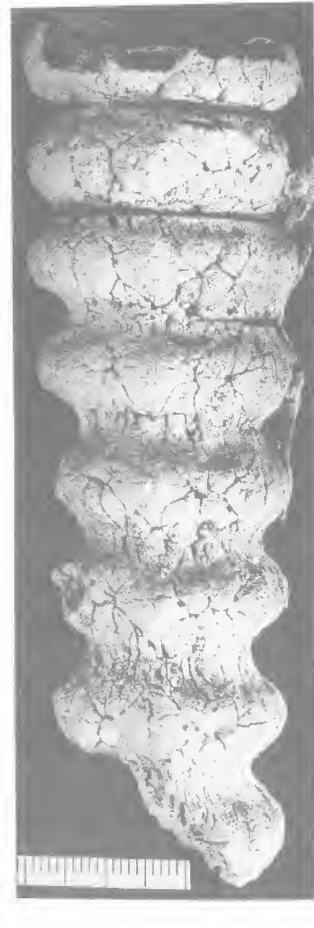
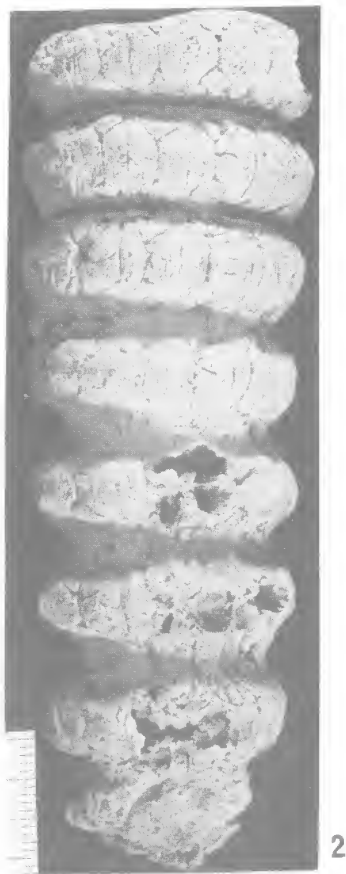


PLATE 3

Scales in mm.

FIGS. 1—6: *Georgina taylori* n. gen., n. sp., $\times 1$, Halfway Dam, Tobermory. All show the contact layer platform covering the annulus in their septal constrictions. Sometimes the septum is adherent to it, and the broken edges of septa can be seen in fig. 6, partly peeled from the contact layer platforms in the posterior septal constrictions of fig. 6. 1—4, F7148, holotype. The pointer on fig. 4 indicates the broken end of a silicified tube (axial canal) in the axial cavity. 5, F7101, paratype, young individual; weathering cracks slightly expanded its posterior end. 6, F7139, paratype, large, well-preserved specimen.

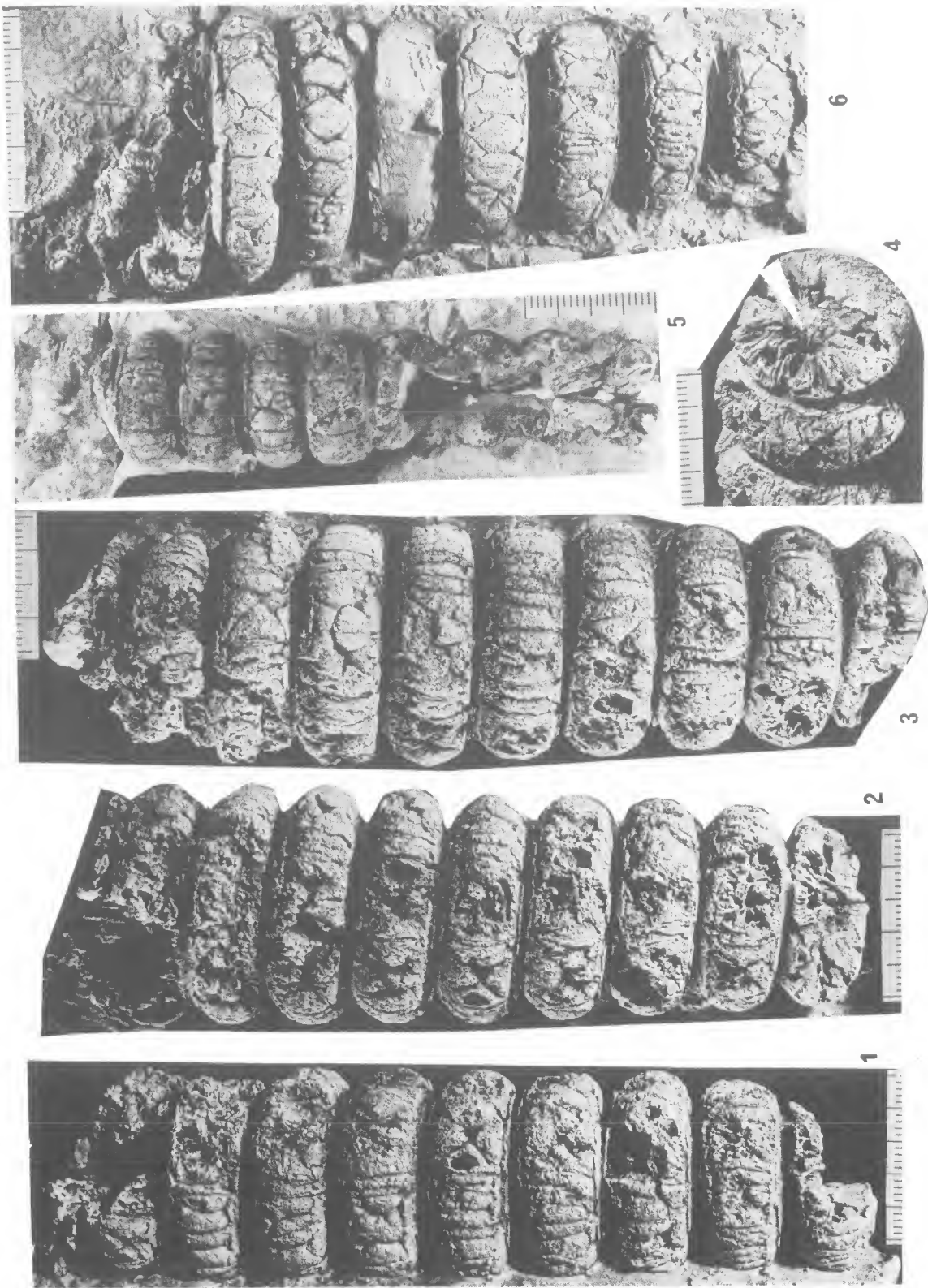


PLATE 4

Scales in mm.

FIGS. 1-7: *Georgina taylori* n. gen., n. sp., paratypes. 1, 2, $\times 1.5$ F7111. 1, longitudinal and oblique transverse sections; pointer at side indicates an engraft sectioned approximately through its dark 'core membrane'. The interannular membranes are occasionally bulged apart by canals. The top indicator, like those in fig. 2, points out the organic walls of the perispatal sinuses between the annulus and (fig. 2) the connecting ring. Only the tips of some engrafts are seen in transverse sections because the section is close to the septum. 3, F7121, partial longitudinal section of large individual showing transverse canal through annulus. 4, F7130, transverse section near septal constriction of specimen with extreme development of radial lamellae. 5, F7091, naturally etched specimen broken through septal neck, radial lamellae most numerous outwardly, axial space irregular, externally the annulus interdigitates with the engrafts, and engraft core membranes are represented by furrows. 6, F7106, $\times 2$, near tangential section through engraft showing core membrane attached to connecting ring. 7, F7149, $\times 2$, longitudinal section passes from one side to the other of the engraft core membrane (inner edge of core membrane at white pointer), a perispatal sinus makes a thin dark line outside the whitish calcite laid on the far side of the core membrane; connecting ring dark, core membrane merges with ring between dark pointers; a second perispatal sinus leads into a passage (segmental sinus) leading inward across the anterior tip of the engraft into the interannulus. The naturally strongly recurved septal neck appears recumbent because the septum was forced down by a lump of detritus.

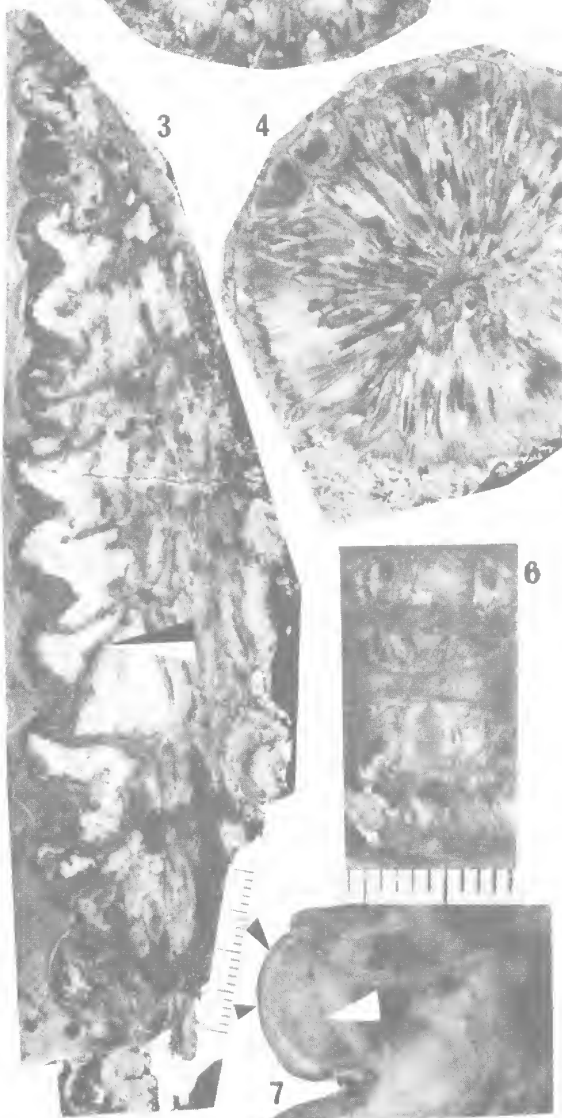
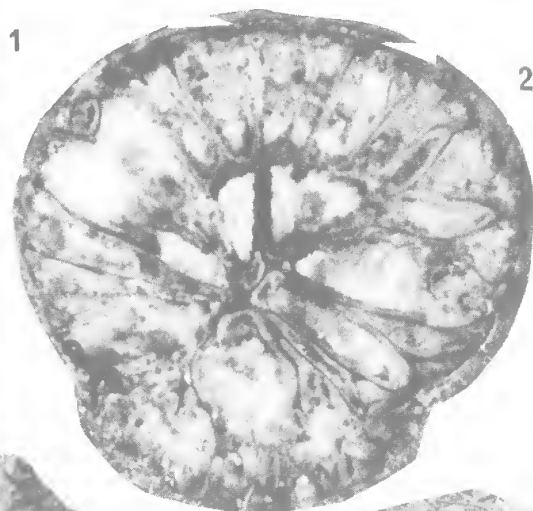
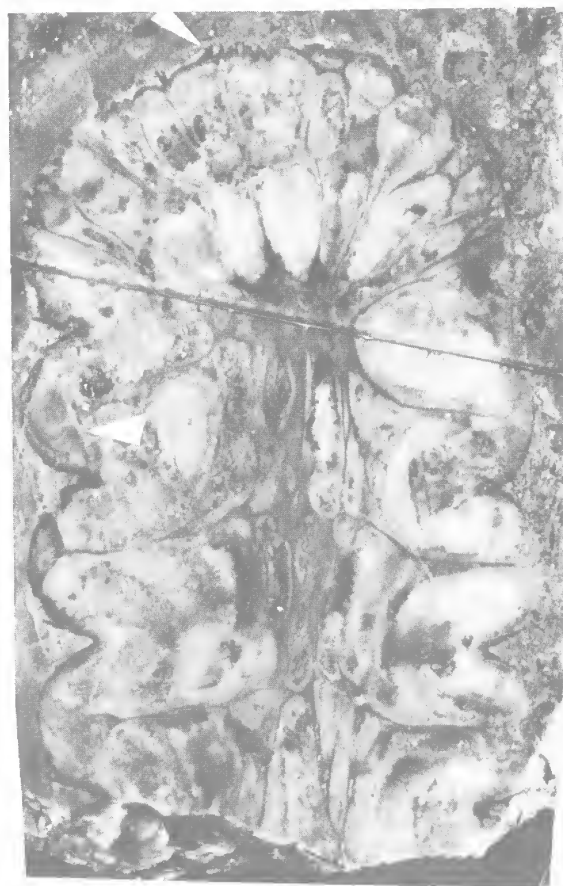


PLATE 5

Figs. 1-8, scales in mm. Fig. 9, scale in cm.

FIGS. 1-5, 8: *Georgina linda* n. gen., n. sp., 1-3, F7176, holotype, 3 km SE. of Linda Ck. and 5 miles NE. of 26 bore, Glenormiston. 1, 2, $\times 1$ oval effect accentuated or induced by wear. 3, $\times 1.5$, longitudinal section showing several axial canals, radial canals, and (lower right) a fan of canal distributaries. 4, $\times 1$, F7177, paratype, locality as above, external view of less worn specimen. 5, 7185, $\times 1$, and 8, F7178, $\times 1.5$, L 319, Toomba Range, paratype transverse sections near interannulus, showing outer ring of engrafts and radial lamellae encircling (5) the base of the anterior cavity and (8) the axial cavity.

FIGS. 6, 7: *Georgina beuteli* n. gen., n. sp., $\times 1$, Halfway Dam. Tobermory. 6, F7219, holotype; traces of very thin contact layers adhere in some of the septal constrictions, and the engrafts are very narrow as in 7, F7220, paratype, (right side truncated by penecontemporaneous erosion).

FIG. 9: *Georgina dwyeri* n. gen., n. sp. $\times \frac{1}{2}$ (scale in cm.), paratype, U.Q. F60014, venter to right.

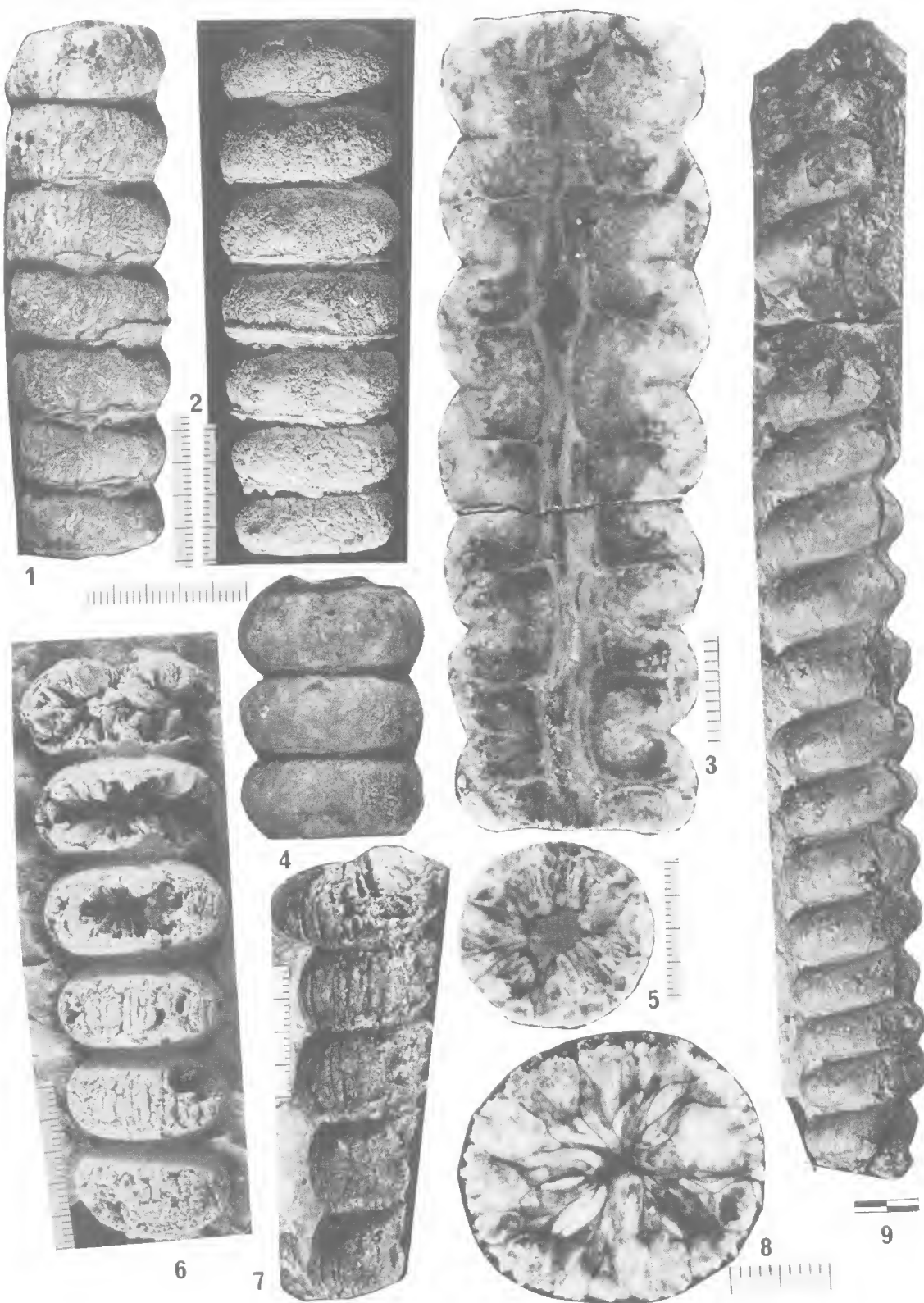


PLATE 6

Scales in mm.

FIGS. 1-6: *Georgina dwyeri* n. gen., n. sp. 1, F7206 paratype, $\times 2$, external view of siphuncle filling showing edges of contact layer platforms, narrow, curved engrafts with core membranes preserved as dark, organic-rich, calcite (c/m), and rock-filled furrows (perispatal sinuses) between the engrafts. Burrows cause shadows at lower right. 2, U.Q. F67153, $\times 1$, paratype, furrows or perispatal sinuses crossing the segment were previously covered by connecting ring. 3-6, U.Q. F66033, $\times 1$, holotype. 3, dorsal view, shows engrafts with core membranes at pointers, and perispatal sinuses between them. 4, lateral view, slightly worn, fragment of septum with neck at pointer. 5, 6, dorso-ventral longitudinal section, dorsal sides adjacent, whitish shell fragment with septal neck lined by dark contact layer at pointers. Similar contact layers coat all the septal constrictions and the pronounced ventral adnation areas. Radial canals occupy the interannulus at the top right 2 segments of fig. 6, and partly occupy the 3rd and 4th interannuli on the left of fig. 5, and its bottom right interannulus. Segmental sinuses can be traced from their external openings at the anterior and posterior of engrafts to the interannulus in the three upper left segments of fig. 6 and the left next to top segment of fig. 5. Axial cavity typically large and straight.

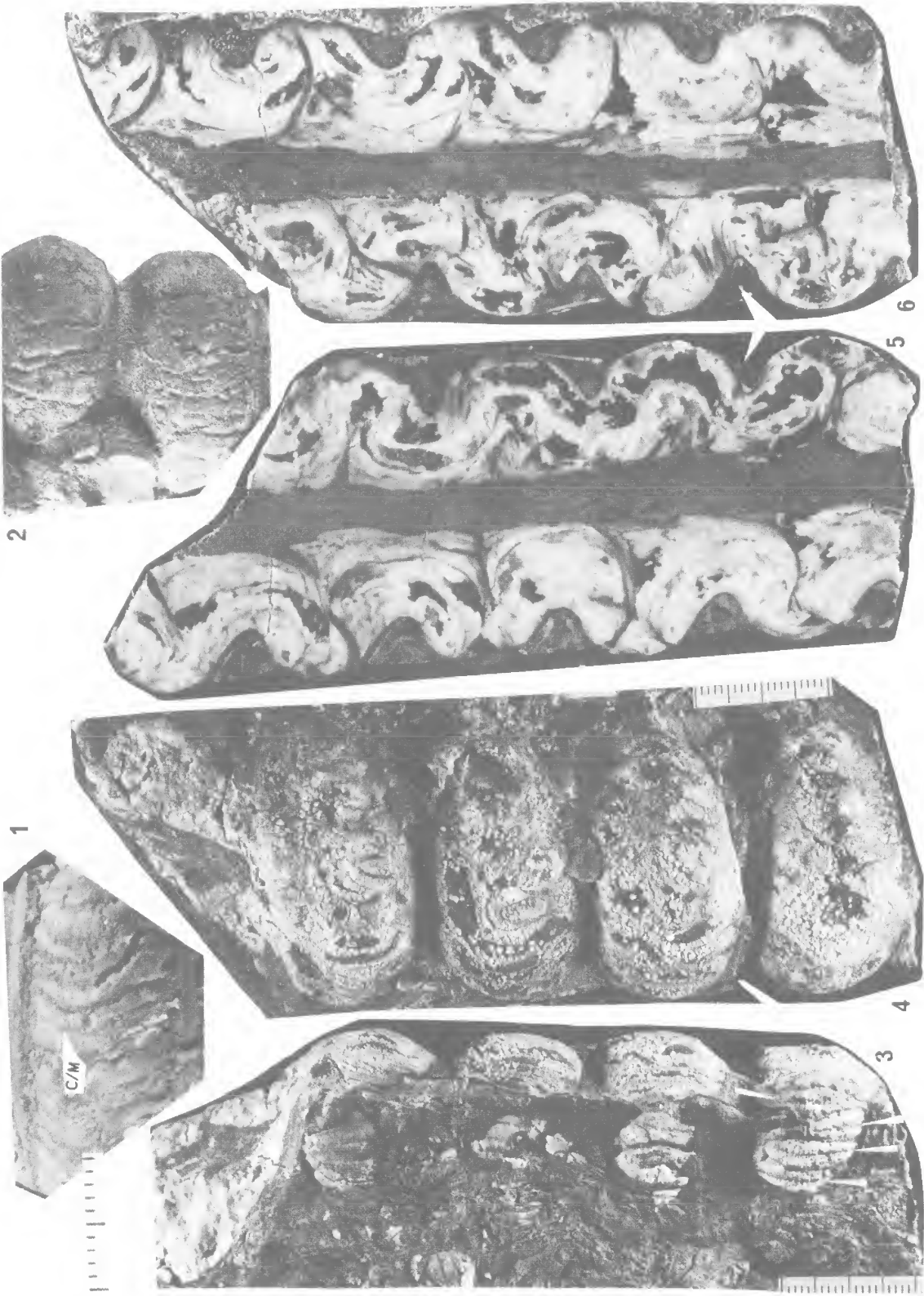
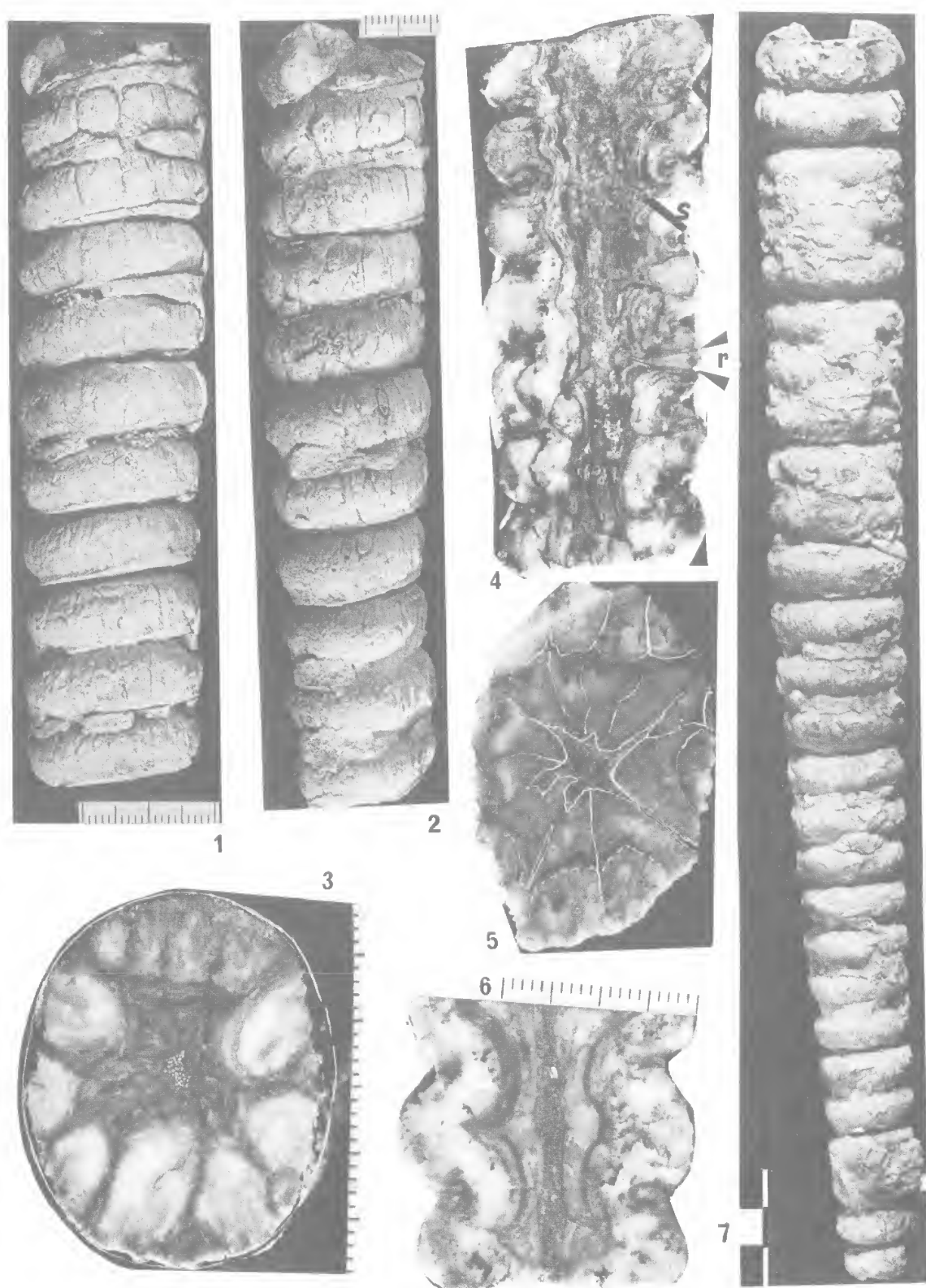


PLATE 7

Figs. 1-6, scales in mm. Fig. 7, scale in cm.

FIGS. 1-7: *Mesaktoceras arachne* n. gen., n. sp., 3 km. E. of Halfway Dam, Tobermory. 1-3, F7187, holotype (includes 6 additional posterior segments), 1, 2, $\times 1$, 3, $\times 2$. White stipple in the centre of 3 covers the rock fill of the axial cavity, section through interannulus shows only engrafts and endocones. 4, F7188, paratype, $\times 1$, longitudinal section, dorsal to left, ventral, right. Annuli reduced on dorsal side relative to ventral, so that engrafts are larger on dorsal. Endocones extend through 6 or more segments. Probably segmental sinus at S. radial canals at r. 5, F7193 paratype, $\times 1.5$, vertical section showing fully developed axial cavity. 7, F7189, paratype $\times 0.6$, longest specimen, flattened in the plane of the paper, incomplete at both ends but with lower part of anterior cavity present.





REVISION OF THE DASYURID MARSUPIAL GENUS *ANTECHINOMYS* KREFFT

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ABSTRACT

Antechinomys is regarded as a monotypic genus containing only *A. laniger* Gould, 1856, which is represented by two distinctive allopatric forms, the nominate form and the 'spenceri' form. The 'spenceri' form differs from the nominate form in its lower nipple number, larger size, and relatively more arid habitat.

It is suggested that *Antechinomys* is at present actively speciating with clines developing between central, relatively more arid regions and the dry but less arid, peripheral, regions of Australia. The differences interpreted here as clinal were formerly regarded as indicators of full specific status for *spenceri* Thomas, 1906.

The closest affinities of *Antechinomys* are clearly with species of *Sminthopsis*, and in particular, *S. crassicaudata*.

The incidence and origin of monotypic marsupial genera in Australia is considered and it is suggested that *Antechinomys* evolved in middle to late Tertiary times in response to the development of widespread relatively arid regions in Australia.

The generic status of *Antechinomys* has not been questioned since 1867 when Krefft proposed the generic name for the species *laniger* Gould, 1856. However, the number of species in the genus has been in doubt. Lidicker and Marlow (1970, p. 216) in their excellent review state in regard to a specimen (BM No. 1939.2997) noted by Tate (1947, p. 125) from Cedar Bay, north Queensland, that this '... disjunct population, if it still survives, may very well represent a separate taxon ...'. Similarly Parker (1973, p. 8) suggests that the north Queensland specimen and specimens from northeastern Northern Territory could represent an undescribed taxon.

Catalogue numbers referred to are abbreviated as follows: BM, British Museum (Natural History); C, National Museum of Victoria; J or JM, Queensland Museum; NTM, Northern Territory Museum (collections in the Arid Zone Research Centre, Alice Springs); SAM, South Australian Museum; WAM, Western Australian Museum; B, Butler collection, Western Australian Museum; 72.3.497 (for example), fossil vertebrate collection, Western Australian Museum.

Measurements have been made only on adults. Points from which cranial measurements have been made are shown in Fig. 1. Tail length as described by Thomas (1888) and appropriate for marsupials has been measured from the vent to the tail tip. This

practice is not universally followed (e.g. Lidicker and Marlow 1970). Condylbasilar length is taken from the posterior edge of the occipital condyles to the posterior edge of the I¹ alveolus. Zygomatic width is not equivalent to Lidicker and Marlow's cranial breadth. Bullar length of Lidicker and Marlow is said by them (p. 214) to be the 'Anterior-posterior length including both alisphenoid and petrotic portions of bullae ...'. Measurements given by them for bullar length of Warburton Range animals indicate that they also involve the inflated portion of the paroccipital process. The same structures are included in bullar length of the present study.

Dental terminology is that used by Archer (1976a). Cranial terminology is shown in Fig. 1 (and follows Archer 1976b). Modern species names are those used by Ride (1970), Laurie and Hill (1954) and Archer (1975).

Family DASYURIDAE Genus *Antechinomys* Krefft, 1866

TYPE SPECIES: *Antechinomys laniger* Gould, 1856
(by monotypy).

GENERIC DIAGNOSIS

Small dasyurids similar to *Sminthopsis* but differ from these in that hallux of hind foot absent; limbs

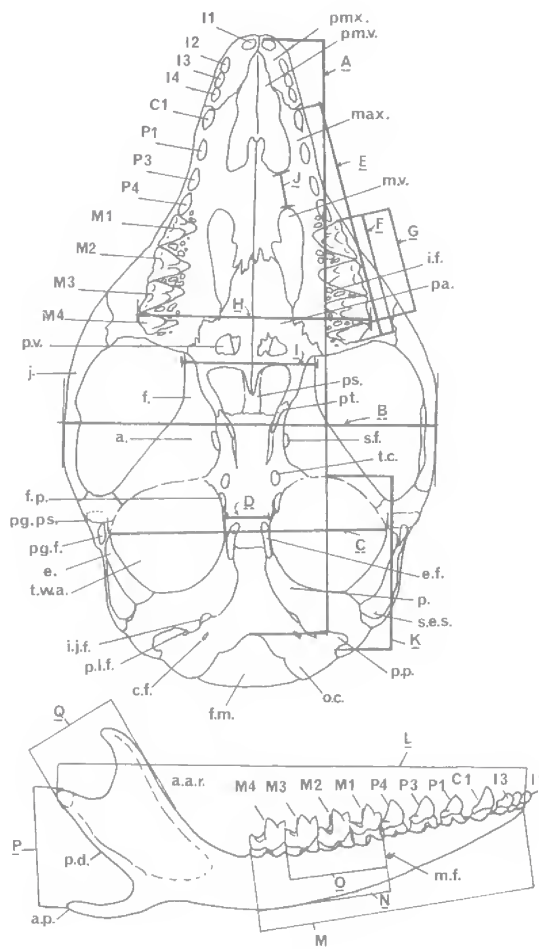


FIG. 1: Terminology and mensuration of skull and dentary of *Antechinomys* (based on the 'spenceri' form of *A. laniger*). a., alisphenoid; a.a.r., anterior border of ascending ramus; a.p., angular process; c.f., condylar (and/or hypoglossal) foramen; e., ectotympanic; e.f., entocarotid foramen; f., frontal; f.m., foramen magnum; f.p., foramen pseudovalve; i.f., interdental fenestrae; i.j.f., foramen of internal jugular canal; j., jugal; max., maxilla; m.f., mental foramen; m.v., maxillary vacuity; o.c., occipital condyle; p., periotic; pa., palatine; p.d., posterior border of dentary; pg.f., postglenoid foramen; pg.ps., postglenoid process; p.l.f., postero-lateral foramen; pm.v., premaxillary vacuity; pmx., premaxilla; p.p., paroccipital process; ps., pre-sphenoid; pt., pterygoid; p.v., palatine vacuity; s.e.s., squamosal epitympanic sinus; s.f., sphenorbital fissure; t.c., transverse canal; t.w.a., tympanic wing of alisphenoid. A-Q, measurements and positions from which they were made. A, basicranial length (BL, Table 1); B, zygomatic width (ZW); C, maximum bullar width (OBW); D, minimum bullar width (IBW) E, C¹-M⁴; F, M¹-4; G, M¹-3; H, R-LM³; I, minimum interorbital width (IO); J, inter-palatal vacuity distance (IPVD); K,

relatively longer; and tail with well-developed distal brush. Differ from all other dasyurids by combination of following characters: squamosal-frontal contact on outside of braincase; nasals not widened posteriorly; palatine vacuities present; tail thin; hind foot narrow, elongate, with interdigital pads fused into single trilobed pad and lacking post-interdigital pads; very small to absent entoconids; no posterior cingulum on upper molars; P4 completely unreduced; C1 premolariform.

GENERIC DISCUSSION

Tate (1947, p. 125) notes that *Antechinomys* '... seems to be derived from the same ancestry as *Sminthopsis*, and from that section of *Sminthopsis* to which *S. crassicaudata* belongs ...'. Additional reasons for regarding *Antechinomys* and *Sminthopsis* to share a common ancestor, include the fact that in both, the squamosal and frontal bones contact on the outside of the cranium, thereby excluding the more normal dasyurid alisphenoid-parietal contact. The structure of the *Antechinomys* talonid also reveals affinity to *Sminthopsis* and particularly *S. crassicaudata*, in that there is an approximation of the entoconid to the lingual end of the hypocristid. Of the two commonly recognized forms of the genus *Antechinomys*, the nominate form is least specialized and hence regarded as structurally ancestral, and it is this form which shows the closest resemblance to *Sminthopsis crassicaudata*.

Antechinomys is considered in the present study to be monotypic. As such, it is one of 30 such marsupial and monotreme genera in New Guinea and Australia (based on reviews by Ride 1970 and Laurie and Hill 1954). Several of these such as *Myrmecobius*, *Thylacinus* and *Notoryctes* are also highly specialized forms in that they do not resemble structurally ancestral marsupials in the supra-familial groups to which they belong. Other monotypic genera such as *Antechinomys*, *Dasyercus*, *Dasyuroides* and *Sarcophilus* are less highly specialized, and structurally similar genera (*Sminthopsis*, *Antechinus* and *Dasyurus* respectively) may be found in the family groups to which they belong. These two sorts of monotypic genera may have had different origins. The fossil history of all these monotypic genera is poorly known, but what is known suggests that, with the

bullar length (includes paroccipital process or paroccipital tympanic wing if developed) (Bul); L, dentary length (DL); M, I₁-M₄; N, M₁-4; O, M₁-3; P, tip of angular process to articular condyle (C-AP); Q, articular condyle to anterior border of ascending ramus (C-AR).

possible exception of *Wallabia*, none has been represented in the past by more than one species at any given time. In the case of the highly specialized forms such as *Myrmecobius*, *Thylacinus* and *Notoryctes*, this seems surprising. These animals are presumably specialized in response to their occupation of unique ecological niches. If they have had a relatively long history to specialize, why have they not also speciated within these unique niches? Why is there only one species of *Myrmecobius* or *Tarsipes* when there are many types of termites and blossoms throughout Australia? In several similar and possibly related lineages elsewhere in the world, speciation has taken place. South American marsupial borhyaenids are structurally very similar to *Thylacinus*, yet at any one time, there were at least two or three genera of borhyaenids. All of these differed from each other at least in size and tooth shape, presumably having adapted to different diets. The origin of the less highly specialized monotypic genera such as *Dasyercus*, *Dasyuroides*, *Caloprymnus* and *Chaeropus* may be late Cainozoic climatic change and the relatively recent production of extensive areas of arid lands in central Australia. These forms may only now be speciating, and it seems likely that *Antechinomys* is a monotypic genus of this sort.

Antechinomys laniger (Gould)

(Figs. 1–2, Plates 8–13)

Phascogale lanigera Gould, 1856, Letterpress for Plate 33.

Antechinomys spenceri Thomas, 1906, p. 331.

TYPES

Phascogale lanigera Gould, 1856.

HOLOTYPE: BM 47.8.14.22 (skin) and 47.12.4.5 (skull), adult male, collected by Sir Thomas Mitchell.

TYPE LOCALITY: Gould (1856, letterpress to plate 33) '... discovered by Sir Thomas Mitchell, during one of his expeditions into the interior of Australia'. Thomas (1888, p. 310)—'New South Wales.'. Tate (1947, p. 125)—'... on the plains between the Murray and Darling Rivers in New South Wales.'.

Antechinomys spenceri Thomas, 1906.

HOLOTYPE: BM 97.11.3.12, skull and carcase in alcohol, obtained by Mr P. Byrne (Spencer 1896, p. 42). Evidently not collected by Spencer on the Horn Expedition as claimed by Thomas 1906, p. 331.

TYPE LOCALITY: Thomas (1906, p. 331)—'Hab. Charlotte Waters, Central Australia.'. Spencer (1896, p. 40) only mentions specimens coming from '... Missionary Plains in the Finke Valley, between the James Range to the south and the McDonnell Ranges to the north.', collected by the Horn Expedition. He gives no locality for additional specimens obtained by Mr P. Byrne (p. 42).

Latter specimens included the only two females obtained (Spencer 1896, p. 42). Holotype must be one of these two females obtained by Mr P. Byrne because Thomas (1906, p. 332) says holotype is one of the specimens referred to by Spencer (1896).

DIAGNOSIS

The species diagnosis is the same as that for the genus until additional species are known.

DESCRIPTION

TAIL: Tail invariably thin. Brush length absolutely longer in 'spenceri' form, but proportionately similar in all populations except Lake Grace where brush is proportionately larger. Tail-vent length exceeds head-body length.

EAR: Ear length in all individuals large, but shorter in nominate than 'spenceri' form.

HIND FOOT: interdigital pads fused as single granular trilobed pad. Toe pads smooth, not granular. Hind foot narrow. Hallux absent. Ventral surface covered by fine hairs, including interdigital pad.

PELAGE MARKINGS: Dark ring around eye. Mystacial vibrissae area of face dark. Middle of forehead with dark patch. Crest of tail dark.

NIPPLE NUMBER: Four, six, eight and ten nipples have been recorded, the latter probably being abnormal. Lidicker and Marlow regard number as distinctive of allopatric forms, 'spenceri' having six and the nominate form eight.

POUCH: Varies in morphology and size with reproductive condition. Woolley (1974) and Lidicker and Marlow (p. 219) review various conditions of pouch.

CRANIUM AND DENTARY: Cranium narrow, and more so in the nominate than 'spenceri' form. Rostrum narrow and elongate. Antero-dorsal part of each frontal convex producing in this area narrow antero-posterior depression in midline of skull. No postorbital processes. Lacrimal bone has wide lateral flanges that extend back over anterodorsal rim of orbit. Commonly lacrimal bones also have posterodorsal flanges. Posterodorsal area of maxilla inflated laterally with development of sinuses. Infraorbital foramen large and commonly perforated ventrally by roots of upper molars. Lacrimal foramina single and on or posterior to rim of orbit. Alisphenoid and periotic tympanic wings variously enlarged. Paroccipital tympanic wing variously inflated to uninflated. All tympanic wings absolutely and proportionately larger in

TABLE 1: ABSOLUTE MEASUREMENTS IN *Antechinomys*.

	N	$\bar{x} \pm T$	OR	s	CV		N	$\bar{x} \pm T$	OR	s	CV
<i>Antechinomys laniger</i> (total modern)						A. l., Tobermory					
BL	27	24.4 \pm .29	21.7-27.1	1.53	6.26	6	23.2 \pm .79	21.7-26.9	1.93	8.34	
ZW	30	14.5 \pm .15	12.9-16.0	0.85	5.84	6	14.1 \pm .47	12.9-16.0	1.16	8.21	
OBW	31	10.4 \pm .14	9.0-11.6	0.77	7.40	6	9.8 \pm .41	9.0-11.6	1.01	10.34	
IBW	30	2.4 \pm .06	1.8- 3.3	0.34	14.28	6	2.4 \pm .11	2.1- 2.7	0.27	11.18	
C ¹ -M ⁴	32	10.2 \pm .10	9.2-11.4	0.58	5.65	6	9.8 \pm .33	9.2-11.4	0.80	8.14	
M ¹ - ⁴	33	5.3 \pm .04	4.6- 5.7	0.26	4.85	6	5.1 \pm .13	4.8- 5.7	0.31	6.07	
M ¹ - ³	37	4.7 \pm .04	4.0- 5.3	0.23	4.77	8	4.6 \pm .06	4.3- 4.8	0.17	3.67	
R-LM ³	31	8.4 \pm .10	7.5- 9.6	0.53	6.31	6	8.1 \pm .32	7.5- 9.6	0.77	9.53	
IO	30	5.5 \pm .06	4.9- 6.0	0.35	6.31	6	5.2 \pm .11	4.9- 5.7	0.27	5.16	
IPVD	31	2.2 \pm .07	1.4- 3.0	0.37	16.61	6	2.0 \pm .10	1.8- 2.4	0.22	11.18	
DL	33	19.7 \pm .20	18.3-21.9	1.13	5.74	6	18.7 \pm .70	17.4-21.9	1.72	9.18	
I ₁ -M ₄	33	11.9 \pm .10	10.8-13.5	0.59	4.88	6	11.8 \pm .33	10.8-13.5	0.82	6.94	
M ₁ - ₄	36	6.1 \pm .05	5.3- 6.5	0.29	4.76	6	5.9 \pm .15	5.6- 6.6	0.37	6.25	
M ₁ - ₃	38	4.5 \pm .04	3.9- 4.9	0.22	4.91	8	4.4 \pm .08	4.2- 4.9	0.23	5.29	
C-AP	31	6.0 \pm .10	5.3- 6.9	0.55	9.15	6	5.7 \pm .25	4.9- 6.9	0.60	10.55	
C-AR	32	3.6 \pm .05	3.2- 4.2	0.28	7.89	6	3.6 \pm .16	3.2- 4.2	0.39	10.76	
A. l., Roper River						A. l., Nullarbor (subfossil)					
BL	3	23.8 \pm .15	23.5-24.0	0.25	1.07	8	10.0 \pm .13	9.3-10.4	0.37	3.72	
ZW	3	14.2 \pm .17	13.9-14.5	0.30	2.11	11	5.2 \pm .06	4.9- 5.5	0.18	3.54	
OBW	3	10.0 \pm .09	9.8-10.1	0.16	1.58	10	4.6 \pm .05	4.3- 4.8	0.17	3.77	
IBW	3	2.9 \pm .06	2.8- 3.0	0.10	3.45	-	-	-	-	-	
C ¹ -M ⁴	3	10.0 \pm .06	9.9-10.1	0.10	1.00	-	-	-	-	-	
M ¹ - ⁴	3	5.2 \pm .06	5.1- 5.3	0.10	1.92	9	2.7 \pm .14	2.0- 3.3	0.42	15.54	
M ¹ - ³	3	4.6 \pm .04	4.5- 4.7	0.07	1.52	31	19.1 \pm .09	18.0-20.2	0.52	2.72	
R-LM ³	3	8.2 \pm .04	8.1- 8.2	0.07	0.85	39	11.2 \pm .04	10.7-11.7	0.25	2.20	
IO	3	5.1 \pm .06	5.0- 5.2	0.10	1.96	37	5.9 \pm .03	5.7- 6.4	0.16	2.79	
IPVD	3	2.5 \pm .25	2.1- 2.7	0.42	16.98	37	4.5 \pm .02	4.2- 4.8	0.15	3.31	
DL	3	19.5 \pm .32	18.9-20.0	0.55	2.83	24	5.7 \pm .04	5.3- 6.0	0.21	3.75	
I ₁ -M ₄	3	11.6 \pm .15	11.3-11.8	0.25	2.20	33	3.7 \pm .04	3.2- 4.3	0.24	6.37	
M ₁ - ₄	3	6.0 \pm .06	5.9- 6.1	0.10	1.67						
M ₁ - ₃	3	4.5 \pm .12	4.3- 4.7	0.20	4.44						
C-AP	3	5.6 \pm .06	5.5- 5.7	0.10	1.79						
C-AR	3	3.6 \pm .06	3.5- 3.7	0.10	2.78						
A. l., Warburton Range						A. l., Lake Grace					
BL	8	25.2 \pm .21	23.0-26.0	0.59	2.36	2	24.8 \pm .22	24.6-24.9	0.32	1.28	
ZW	9	14.7 \pm .17	14.1-15.6	0.50	3.40	2	14.8 \pm .00	14.8-14.8	0.00	0.00	
OBW	9	11.0 \pm .12	10.5-11.5	0.38	3.42	2	10.0 \pm .00	10.0-10.0	0.00	0.00	
IBW	9	2.1 \pm .06	1.8- 2.3	0.17	8.07	2	3.3 \pm .00	3.3- 3.3	0.00	0.00	
C ¹ -M ⁴	9	10.5 \pm .13	10.1-11.1	0.39	3.67	2	10.5 \pm .16	10.3-10.6	0.22	2.13	
M ¹ - ⁴	9	5.4 \pm .05	5.1- 5.6	0.16	3.00	2	5.5 \pm .07	5.4- 5.5	0.10	1.82	
M ¹ - ³	10	4.8 \pm .04	4.7- 5.0	0.12	2.59	2	4.8 \pm .00	4.8- 4.8	0.00	0.00	
R-LM ³	9	8.8 \pm .08	8.4- 9.0	0.25	2.90	2	8.7 \pm .00	8.7- 8.7	0.00	0.00	
IO	8	5.8 \pm .05	5.7- 6.0	0.13	2.25	2	5.8 \pm .07	5.7- 5.8	0.10	1.72	
IPVD	9	2.4 \pm .10	2.0- 2.9	0.30	12.41	1	2.7 \pm .00	2.7- 2.7	0.00	0.00	
DL	9	20.1 \pm .19	19.3-20.9	0.58	2.88	2	19.9 \pm .43	19.2-20.6	0.86	4.32	
I ₁ -M ₄	9	12.1 \pm .11	11.7-12.8	0.33	2.69	2	12.3 \pm .20	12.1-12.5	0.28	2.30	
M ₁ - ₄	9	6.2 \pm .06	5.7- 6.5	0.19	3.12	2	6.2 \pm .00	6.2- 6.2	0.00	0.00	
M ₁ - ₃	10	4.5 \pm .05	4.2- 4.7	0.15	3.31	2	4.6 \pm .07	4.5- 4.6	0.10	2.17	
C-AP	8	6.5 \pm .08	6.2- 6.7	0.22	3.44	1	5.6 \pm .00	5.6- 5.6	0.00	0.00	
C-AR	9	3.7 \pm .06	3.2- 4.0	0.17	4.48	1	3.3 \pm .00	3.3- 3.3	0.00	0.00	

'spenceri' than nominate form. Ectotympanic variously enclosed by alisphenoid tympanic wing. Sphenorbital foramen separated from foramen rotundum by variously wide bar of alisphenoid. Foramen rotundum larger than transverse canal and entocarotid foramina. Entocarotid canal variously developed, being often complete enough to obscure ventral view into cranium in 'spenceri' form, while leaving broad direct ventral opening into cranium in nominate form. Transverse canal large but variously wide depending on development of tympanic wings.

Foramen pseudovale varies in width and length, being narrow in 'spenceri' form and wider in nominate form. Internal jugular canal formed between periotic and basioccipital has near vertical mesial wall in 'spenceri' form, less vertical wall in nominate form. Basioccipital keeled antero-ventrally in midline. In some specimens (e.g. WAM M2368) periotic has small bony process which extends antero-mesially across posterior lacerate foramen towards internal jugular canal foramen. Pterygoid or hamular process, when complete, generally has tuberosity, or expanded tip at distal end. Palatal spine well-developed when complete, being almost as long as hamular process of pterygoid. All palatal vacuities very large in length and width. Inter-dental fenestrae numerous and palate between consecutive molars commonly reduced to lattice of bony trabeculae. Externally, squamosal contacts frontal excluding parietal-alisphenoid contact. Nuchal crest commonly produced between occipital and parietal bones. Occasional interparietal ossifications present.

Dentary distinctive in having almost parallel anterior edge of ascending ramus and posterior edge of dentary. Articular condyle high and much closer to tip of ascending ramus than tip of angular process. Dentary slender and very shallow at anterior end. Symphysis short, back to level of P_3 in adult, and unfused (contrary to suggestion of Tate 1947, p. 125).

DENTITION: I^1 just taller-crowned than I^4 , subequal to I^3 , and larger than I^2 . I^4 crown larger than I^3 crown which is subequal to I^2 crown. I^{2-4} with extremely reduced to absent posterior cusps. I^1 and I^2 and I^4 and C^1 separated by diastemata. C^1 premolariform with (in unworn state) distinct

anterior and posterior cingular cusps. C^1 subequal to or just larger in crown height and length to P^1 , but subequal to or smaller than P^3 , and conspicuously smaller than P^4 . C^1 without buccal and lingual cingula. P^1 with anterior and posterior cingular cusps and no buccal cingulum. Lingual cingulum variously developed from very reduced to absent. P^3 with anterior and posterior cingular cusps. P^3 frequently has cingulum developed around tooth except just beneath lingual and buccal position of paracone tip. P^1 has small anterior and large posterior cingular cusps. P^4 has small anterior and large posterior cusps. P^4 also have lingual swelling in crown midway along length serving as buttress for paracone. P^4 cingula distributed as in P^3 . DP^4 three-rooted, with six to seven cusps: low protocone, low stA, large stD, variably developed tiny stE, large paracone and large metacone immediately lingual to stD. DP^4 metacrista well-developed. Paracrista absent (presumably result of lack of discrete stB). Pre- and post-protocrista very tiny. All dP^4 cusps sustain wear with age. P^4 slightly taller-crowned than P^3 which is conspicuously larger than P^1 . DP^4 crown as long as P^3 but shorter-crowned than any premolar. M^{1-4} relatively wide, among widest in all dasyurids. Homologue of stA present but indistinguishable from buccal end of anterior cingula M^{1-4} . StA M^1 relatively most distant from stB. StB present M^{1-4} . StD largest M^1 , smallest M^3 . StC absent. StE small and present M^{1-3} either as small cusp or buccal crest connected to posterior flank of stD. Paracone gradient increases from M^1 to M^4 . Metacones M^3 and M^1 subequal in size and smaller than M^2 . Variably present or distinguishable metacone M^4 . Protocones M^1 and M^2 subequal and larger than protocone M^3 which is in turn larger than protocone M^4 . Anterior cingula M^{1-4} confined to antero-buccal corner of tooth and not connected to preprotocrista. No posterior molar cingula. Paracrista increases in size from M^1 to M^4 . Metacristae M^1 and M^3 subequal in length and smaller than metacrista M^2 . Protoconule absent. Metaconule generally absent but sometimes present on M^4 postprotocrista.

I_1 taller-crowned than I_3 which is taller-crowned or subequal to I_2 . I_3 with variably present small posterior lobe generally abutting anterior edge of C_1 . C_1 generally lacks anterior cingular cusp but

Abbreviations: BL, basicranial length; ZW, maximum zygomatic width; OBW, outside bullar width; IBW, inside bullar width; IO, minimum interorbital width; IPVD, inter-palatal vacuity distance; DL, dentary length; C-AP, articular condyle of dentary to tip of angular process; C-AR, C to anterior border of ascending ramus; N, sample number; \bar{X} , sample mean; r , standard error of the mean; OR, observed range; S, standard deviation; CV, coefficient of variation. Locality names abbreviated as follows: Tobermory, N.T.; Roper River, N.T.; Nullarbor, W.A., surface of caves; Warburton Range, W.A.; Lake Grace, W.A.

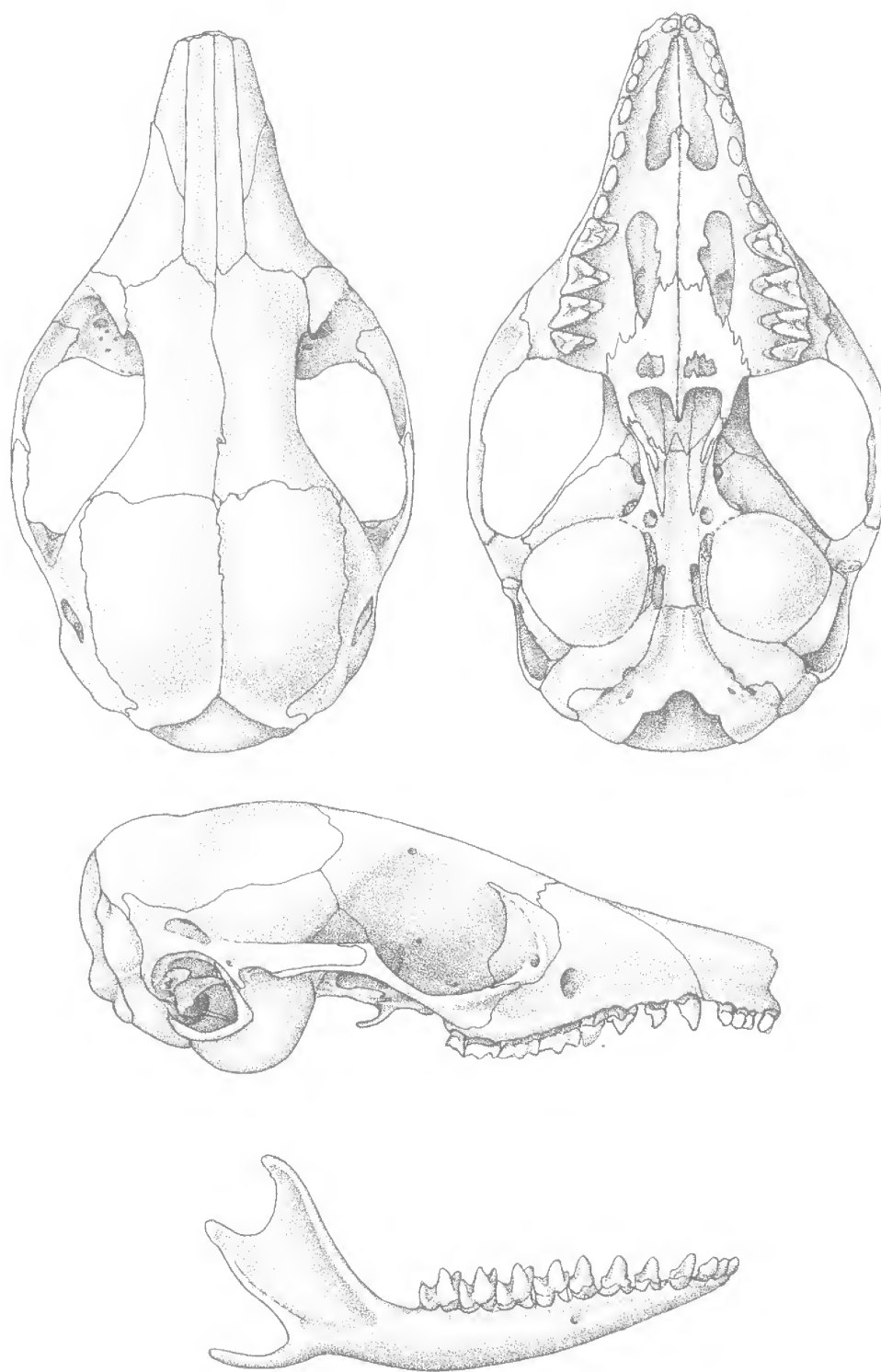


FIG. 2: *Antechinomys laniger* ('spenceri' form). Drawings based on photographs and specimen B1654.

has posterior cingular cusp. C_1 has moderately well-developed buccal and lingual cingula. C_1 crown taller than P_1 crown but shorter than P_3 crown. P_{1-4} generally have small anterior cingular cusps but moderate to large posterior cingular cusps. P_{1-3} have very narrow cingula surrounding crowns. P_4 lacks cingula at base of protoconid. DP_4 has one principal cusp, the protoconid, and one secondary cusp, the hypoconid. DP_4 crown surrounded by narrow cingulum. On posterior flank of protoconid may be miniscule remnant of homologue of metaconid. DP_4 hypoconid connected via posterior hypocristid to postero-lingual cingular cusp possibly representing hypoconulid. Paraconids M_{1-4} increase in size posteriorly. Metaconid and protoconid increase in height posteriorly. Metaconid and protoconid of M_3 subequal to those cusps on M_4 . Hypoconids M_{1-4} subequal in height. Cusps on lingual side of talonid complex. Although normally only an entoconid occurs, in some specimens (e.g. WAM M2860) there are three cusps: small cusp basal to metaconid called here a metastylid; another small cusp, sometimes connected to metastylid by crest, called here an entostylid; and third cusp immediately buccal to entostylid, connected to lingual end of posterior hypocristid, called here the entoconid. Homology of so-called entostylid in doubt and it may in fact be entoconid of other dasyurids. Generally, metastylid M_1 largest and size of cusp decreases posteriorly to M_3 . Generally, size of so-called entostylid smallest M_1 and size increases posteriorly to M_3 . These inverse gradients commonly occur in same specimen (e.g. J23615). Paracristids and metacristids increase in length from M_1 to M_3 . Paracristid and metacristid M_4 subequal to same of M_2 . Trigonid M_1 narrower than talonid. Trigonids and talonids M_{2-3} subequal in width. Talonid M_4 very narrow and high with prominent crest possibly homologous with cristid obliqua of M_{1-3} . Lingual face of cristid obliqua M_4 concave and bounded lingually by basal crest or series of tiny cusps possibly in part homologous with metastylids and entostylids of M_{1-3} .

HABITAT

Lidicker and Marlow describe the habitat in north central N.S.W. and south central Qd of the nominate form as savannah, grass ground cover being interspersed with open areas. Evidently hollow logs and stumps are used as retreats. Troughton (1967) notes that this form is said by Krefft to eat mice in captivity. Parker (1973) notes that animals from the Roper River area apparently inhabit salt-marsh near the river's mouth.

The habitat of the 'spenceri' form is better known. Philpott and Smyth (1967) note the capture of one individual on undulating gibber plain 26 km west of Glengyle Homestead, south-western Queensland. Lidicker and Marlow (p. 227) state that the 'spenceri' form '. . . seems to inhabit a variety of open, tree-less, habitats over much of arid Australia.'. In western Queensland they captured individuals on a sparsely vegetated gravelly plain, in association with *Dasyuroides byrnei* and *Notomys cervinus*. Ride (1970) notes that in the Warburton Range area, Miss P. Robertson found one individual in a burrow. A similar observation was also made by Le Souef and Burrell 1926, who claim the burrows were those of *Notomys*. Ride (1970), regards the instance he notes as unlikely to involve a burrow of a native mouse because the Warburton Range burrow had only one entrance. Another specimen of the 'spenceri' form noted by Ride was captured in a trap-door spider's burrow. Parker (1973, p. 8) notes of these animals in the Northern Territory that they are 'Not uncommon following good seasons, in a variety of country, including sandhills, mulga and gidgea woodland, mitchell grass plains and gibbers'. Finlayson (1961) notes that in 1953-6 the 'spenceri' form was frequently being brought by cats at night into homesteads in the Everard and Musgrave Ranges area of central Australia. Collins (1973) notes aspects of the behaviour of this form in captivity, as does Happold (1972).

Nobody has specifically stated that under normal circumstances individuals of the 'spenceri' form (or the nominate form) have been known to kill small vertebrates for food. On the contrary, Ride (1970, p. 126) says 'The animals which I have kept did not touch meal worms at first, but would eat cockchafer larvae, and large moths and spiders. Lizards placed in a box with them were left untouched.'. Krefft (noted by Troughton 1967) claimed the nominate form, when put into a box with a number of rodents, at once attacked them. This is not necessarily indicative of a normal habit. A *Planigale* will just as readily attack a finger of a hand if it is thrust into a confined space with the frightened animal, but this presumably does not indicate an intention to eat the hand.

REPRODUCTION

Lidicker and Marlow (p. 219) note that a female of the nominate form, taken in late May from El Trune Stn, New South Wales, showed '. . . initial pouch development.'. They also note probable changes in pouch morphology as a function of reproductive condition.

Lidicker and Marlow state that two females of the 'spenceri' form examined from the Warburton Range area had young. WAM M5871, collected 2 November 1963, had three young, and WAM M5886, collected mid-August 1973, had six. Ride (1970) says this form appears to breed in winter. Happold (1972) notes the capture in southwestern Queensland of a female of the 'spenceri' form with pouch young, in late October 1968. Collins (1973) notes a female (locality unspecified) of this form with very small pouch young caught in late October. Two captive individuals (pers. comm. Stanley to Collins) developed pouches in mid-July and by August exhibited behaviour and pouch development indicative of the onset of oestrus. Woolley (1973) notes that birth of the 'spenceri' form is estimated to occur in November. These observations suggest the 'spenceri' form may be monoestrous in apparent contrast to the sympatric species of *Sminthopsis*, *S. crassicaudata* and *S. macroura*.

DISCUSSION OF *Antechinomys laniger*

CONCEPT OF ONE SPECIES IN *Antechinomys*

There is a blurring of characters previously considered (e.g. by Lidicker and Marlow) to be diagnostic of species, in several populations of *Antechinomys*. In particular animals from Tobermoray and the Roper River area of the Northern Territory, from the Nullarbor and Lake Grace area of Western Australia, and Cedar Bay, in Queensland show characteristics which do not clearly enable them to be classified as either *spenceri* or *laniger* in terms of the species concepts employed by Lidicker and Marlow. As a result, two alternative conclusions were considered here: Either the 'aberrant' forms represent yet additional taxa; or they indicate that *spenceri* should be regarded as a form of *A. laniger*, which is a somewhat variable, widespread species. The first alternative seemed the least likely because in at least one population (Tobermoray) morphological and size variation is comparable to that exhibited by *Antechinomys* as a whole. The second alternative seemed more reasonable. Several other dasyurid species have comparable wide geographic ranges of variation such as *Sminthopsis macroura*, *S. crassicaudata*, *Dasyurus cristicauda*, and *Antechinus macedonellensis*. The only particularly unusual areas of distribution for such central Australian wide-ranging species are the Roper River and Cedar Bay localities. However, on morphological grounds, there is no sound basis for distinguishing the Roper River animals from the more central Tobermoray animals. Further, there are suggestions of clines

(some morphological aspects of which are noted by Lidicker and Marlow, p. 223) correlatable with aridity. For example, the Cedar Bay specimen, referred in previous studies to the nominate form, and specimens from the Western Australian Warburton Ranges, referred in previous studies to the 'spenceri' form, are morphologically dissimilar. However, geographically intermediate specimens from Roper River Mission and Tobermoray, Northern Territory, show intermediate conditions. As a result, it has been concluded here that small individuals with small alisphenoid tympanic wings (the nominate form) are distributed geographically around forms which are larger, but which also have relatively large tympanic wings ('spenceri' form), probably because of adaptation to relatively more arid habitats.

CHARACTERS PREVIOUSLY USED TO RECOGNISE MORE THAN ONE SPECIES: Lidicker and Marlow summarize (their table 1) results of their comparisons which lead them to conclude that there are two species. In the present study these and other characters have been used to compare specimens from localities unknown to them. The results of this comparison are shown in Table 2.

Characters regarded by Lidicker and Marlow to demonstrate species differences are as follows:

(1) Tail length and brush length: Lidicker and Marlow consider the length of the caudal brush (pencil) to be one of the most diagnostic measurements in *Antechinomys*, their calculated mean for individuals of the nominate form (not including the Cedar Bay specimen) being 51.8 mm and their mean of the 'spenceri' form being 61 mm (observed range being 56 to 70). The only two specimens of Warburton Range *Antechinomys* ('spenceri' form) measured in the present study have a mean brush length of 54.3 mm with a range of 52.8–55.8. This almost certainly overlaps the range of the nominate form. Other isolated individuals and populations examined in the present study demonstrate considerable variation in brush length, although there is a tendency for absolutely larger brush lengths to occur in more inland animals. An exception is the animals from Lake Grace which, although certainly in a less central situation than the Warburton Range, have a mean brush length of 70.1 mm. When brush length is expressed as a proportion of total tail length, the mean of individual animals from the Warburton Range and Tobermoray is the same, 0.44. In fact all the means except that of Lake Grace animals, have comparable values, including that for the nominate form and animals from southern Queensland, considered by Lidicker and Marlow to represent the nominate form (the

latter 'mean' was determined using Lidicker and Marlow's figures for brush length and tail length). Evidently, despite apparent differences in absolute brush length, most *Antechinomys* have a reasonably constant proportion of their tail taken up by a brush.

(2) Hind foot length: From Lidicker and Marlow's figure 2, the mean standardized hind foot length of the typical form is 28.5 mm (not including the Cedar Bay specimen which is 26.2 mm). The same measurements given by them for the 'spenceri' form range from 30.0 to 31.6 mm. Foot measurements taken in this study from dry and alcohol specimens were standardized as suggested by Lidicker and Marlow (p. 213) and are shown in Table 2. The mean (27.7) given in the present study for the Lake Grace animals differs from that (30.0 mm) given by Lidicker and Marlow. The labels of WAM M2230 and M2368 both give '3.0' for hind foot measurements. Dry measurements (*su*) made on both specimens give 28.8 for WAM M2230 and 23.8 for WAM M2368. Standardizing these by adding 1.4 mm, the values are 30.2 and 25.2 mm and the mean, 27.7 mm. Evidently mean foot length of *Antechinomys* increases in central Australian localities, being smallest in peripheral, relatively less-arid areas such as Roper River, Lake Grace and New South Wales.

(3) M_{1-3} and M^{1-4} : The mean M_{1-3} length in *Antechinomys* shows only slight differences for populations referable to the 'spenceri' and nominate forms. Only the Cedar Bay individual stands out by being 0.3 mm smaller than any other specimen of *Antechinomys*. M^{1-4} is used by Lidicker and Marlow as a basis for comparison. The difference in mean values and observed ranges are similar to those of M^{1-3} except that the mean of animals from the Nullarbor sample is smaller than that of animals referable to the 'spenceri' form from central Western Australia. Mean M^{1-4} given by Lidicker and Marlow for the nominate form is 5.1 mm. This contrasts with the higher (5.4–5.9) mean values for populations they consider to represent the 'spenceri' form. Mean M^{1-4} value for the Tobermoray population is 5.1 mm. One Tobermoray male has a value of 5.7, which exceeds by 0.3 any specimen of the nominate form measured by Lidicker and Marlow.

(4) $C_1 - P_1$ space and $C_1 - P_1$ alveolar distance: Lidicker and Marlow conclude that the nominate form has a $C_1 - P_1$ space (presumably shortest distance between C_1 and P_1 crowns) of less than 0.2 mm, while the 'spenceri' form has a length of 0.2 to 0.5 mm. This character appears to be somewhat

variable in samples examined in the present study. The highest values occur in individuals from southwestern Queensland and the Warburton Range, but the individual means of all non-Queensland *Antechinomys* populations were below 0.2 mm. $C_1 - P_1$ alveolar distance (maximum distance between anterior edge of C_1 and posterior edge of P_1 alveoli) was measured in order to allow comparison with the large sample of Nullarbor specimens which, in most cases, lack C_1 . Means of specimens from the Warburton Range and Lake Grace are identical (2.38 mm). The only very different specimens are several from southwestern Queensland with high values (2.75 and 2.80 mm). The Nullarbor sample (37 individuals) had the lowest mean value (1.99 mm). These two measurements are of doubtful value. It is probable that even though all specimens measured were adult, the size of this feature will increase with age.

(5) Tympanic wing (or bulla) size, absolute and as a ratio: An examination of the distribution of absolute tympanic wing size indicates that means of animals from New South Wales, Cedar Bay, Roper River area, Tobermoray and Lake Grace are all relatively small. Means of animals from central Australia are high. There is also overlap in the observed ranges between central Australian and Tobermoray specimens. Alisphenoid tympanic wing (or bulla) width (BW, Table 2) is determined by subtracting the minimum distance (IBW, Table 1) between the left and right alisphenoid tympanic wings from the maximum distance (OBW, Table 1) between the left and right alisphenoid tympanic wings (the latter is measured from dorso-lateral points on the tympanic wing of the alisphenoid mesial to the glenoid fossa of the squamosal). BW is thus the composite width of both alisphenoid tympanic wings. The BW/zygomatic width (ZW, Tables 1–2) ratio is an estimate of the amount of cranial width represented by tympanic wing development. Specimens from the Warburton Range area have a very high mean, matched only by isolated animals from southwestern Queensland. Specimens from Lake Grace have a very low figure, even lower than the Cedar Bay specimen. In this regard, specimens from Roper River and Cedar Bay are similar, both having relatively small tympanic wings. About the same degree of similarity exists between Roper River and Tobermoray specimens as between the latter and specimens from central Western Australia, although the central specimens have the largest tympanic wing development. There appears to be a trend with larger tympanic wings occurring in progressively more arid areas.

(6) Cranial height: This character appears to vary in the same way as tympanic wing size and reflects the fact that cranial height, as described by Lidicker and Marlow (1970), involves maximum vertical height of the alisphenoid tympanic wings.

(7) Rostral width, length, and a relative ratio: Rostral width is shown by Lidicker and Marlow (their table 1) to be smaller in the nominate form, with no overlap in observed range between the 'spenceri' and the typical forms, except in the isolated Cedar Bay specimen. Examination here of larger and additional samples reveals a broad overlap between most populations of *Antechinomys*. Rostral length shows greater variation and even broader overlap in observed range between all populations. The ratio of RW/RL has also been examined. Two sorts of values are presented in Table 2. The first is the mean of the ratios for specimens examined in this study. The second is an approximated mean determined by using the means for rostral width and rostral length given by Lidicker and Marlow (their table 1). At least in the case of specimens from Warburton Range, the resultant figure is the same. In any case, differences for any given population are slight. In particular it should be noted that the 'mean' (0.35) of specimens referable to the nominate form is the same as that for specimens referable to the 'spenceri' form from the Warburton Range. This indicated that although slight differences occur in absolute measurements, proportions of the rostrum are clearly similar in both forms.

(8) Other characters: Most characters examined in this and Lidicker and Marlow's study show marked overlap in range in specimens referable to the 'spenceri' and nominate forms.

Of the characters used by Lidicker and Marlow to diagnose species of *Antechinomys*, nipple number alone seems not to overlap in the two forms, with the nominate form having eight to ten and the 'spenceri' form, four to six.

RECOGNIZABLE FORMS OF *Antechinomys laniger*

There seems little point in recognizing more than two (or possibly three if the Cedar Bay specimen is regarded as unique) forms of *A. laniger*. Use of the name 'spenceri' to distinguish the central Australian form is not to be interpreted as recognition here of its subspecific status because no attempt has been made to determine the statistical validity of the forms of *A. laniger* as subspecies.

The Nullarbor population has not been referred here to any particular form because material available for examination is incomplete. Lundelius

and Turnbull (1975) refer it to *spenceri* but note that the differences involved are slight and of dubious diagnostic value.

The nominate form (Plates 8–10, 12A–C, 13C–F) may be distinguished from the 'spenceri' form by its relatively smaller size, narrower palate, narrower skull, shorter caudal brush, shorter ears, shallower skull, smaller tympanic wings, and possession of eight nipples (this latter character has not been checked in all populations). Its range includes northern Victoria, New South Wales west of the Divide, south central Queensland, the Roper River Mission area and Tobermoray in the Northern Territory, the Lake Grace area of Western Australia, and the Cedar Bay in northeastern Queensland. The holotype of *Phascogale lanigera* Gould occurs within this range.

Because the nominate form is structurally ancestral and most similar to species of *Sminthopsis*, it is possible that only populations referable to the 'spenceri' form have markedly diverged from the ancestral stock. However, it is also possible that some populations referred here to the nominate form (such as those from Tobermoray) are derivatives of the 'spenceri' form which have secondarily come to resemble the nominate form by re-adapting to relatively less-arid areas.

The 'spenceri' form (Figs. 1–2, Plates 11, 12D–E, 13A–B) may be recognized by its relatively larger size, wider palate, wider skull, longer caudal brush, longer ears, deeper skull, larger bullae, and possession of six nipples. Jones (1923) gives a good description of this form which is supplemented by the description given by Lidicker and Marlow. The range of this form includes the southern Northern Territory, central Western Australia, northern South Australia, and southwestern Queensland. The holotype of *Antechinomys spenceri* Thomas evidently comes from Charlotte Waters, within this range.

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PLATE 8

A–D, *Antechinomys laniger*, SAM M1804, adult, Roper River, N.T.
A, $\times 3.9$. B–D, $\times 2.7$.

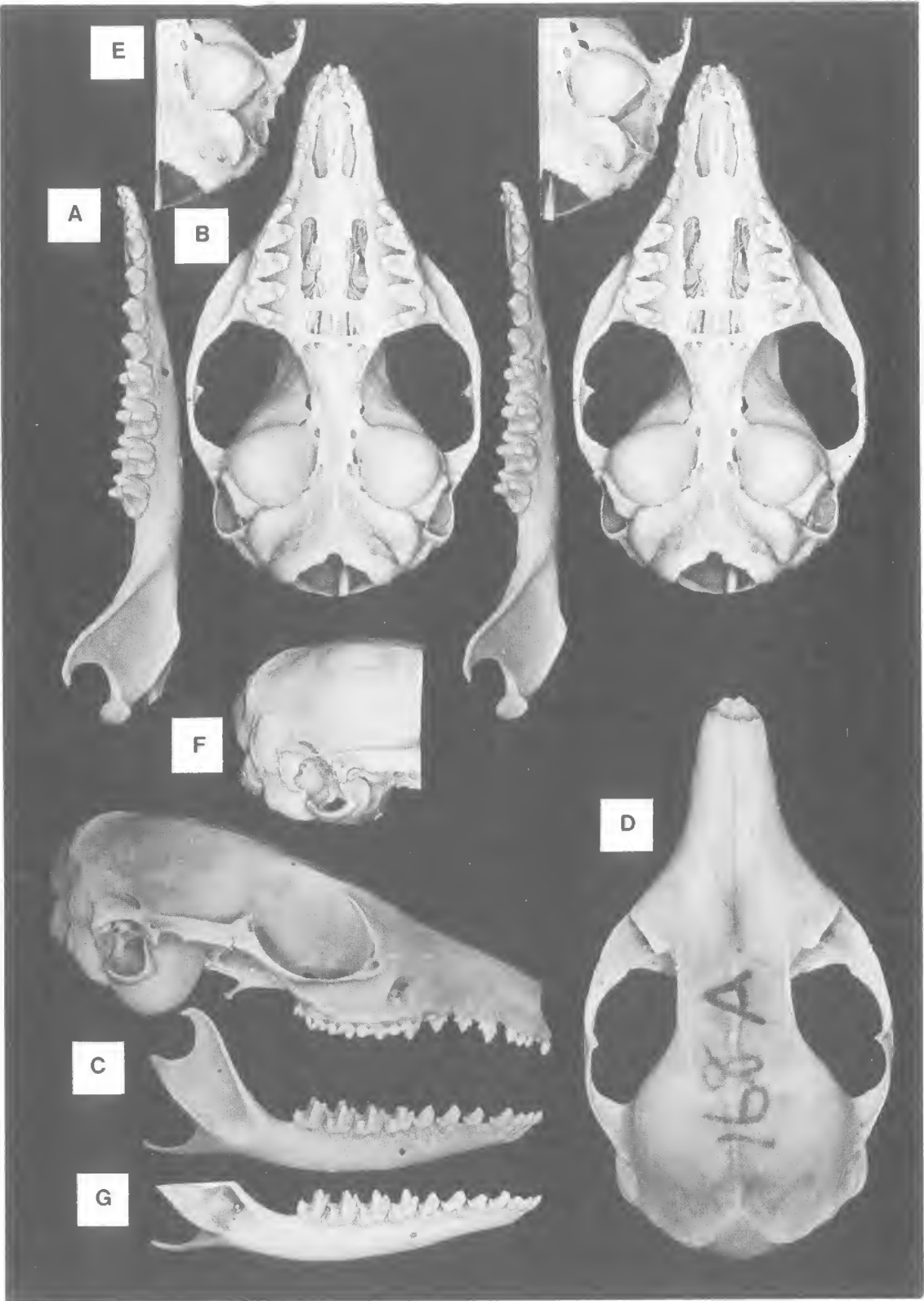


PLATE 9

A-D, *Antechinomys laniger*, WAM M2368, adult, Lake Grace, W.A.
A, $\times 3.9$. B-D, $\times 2.7$.

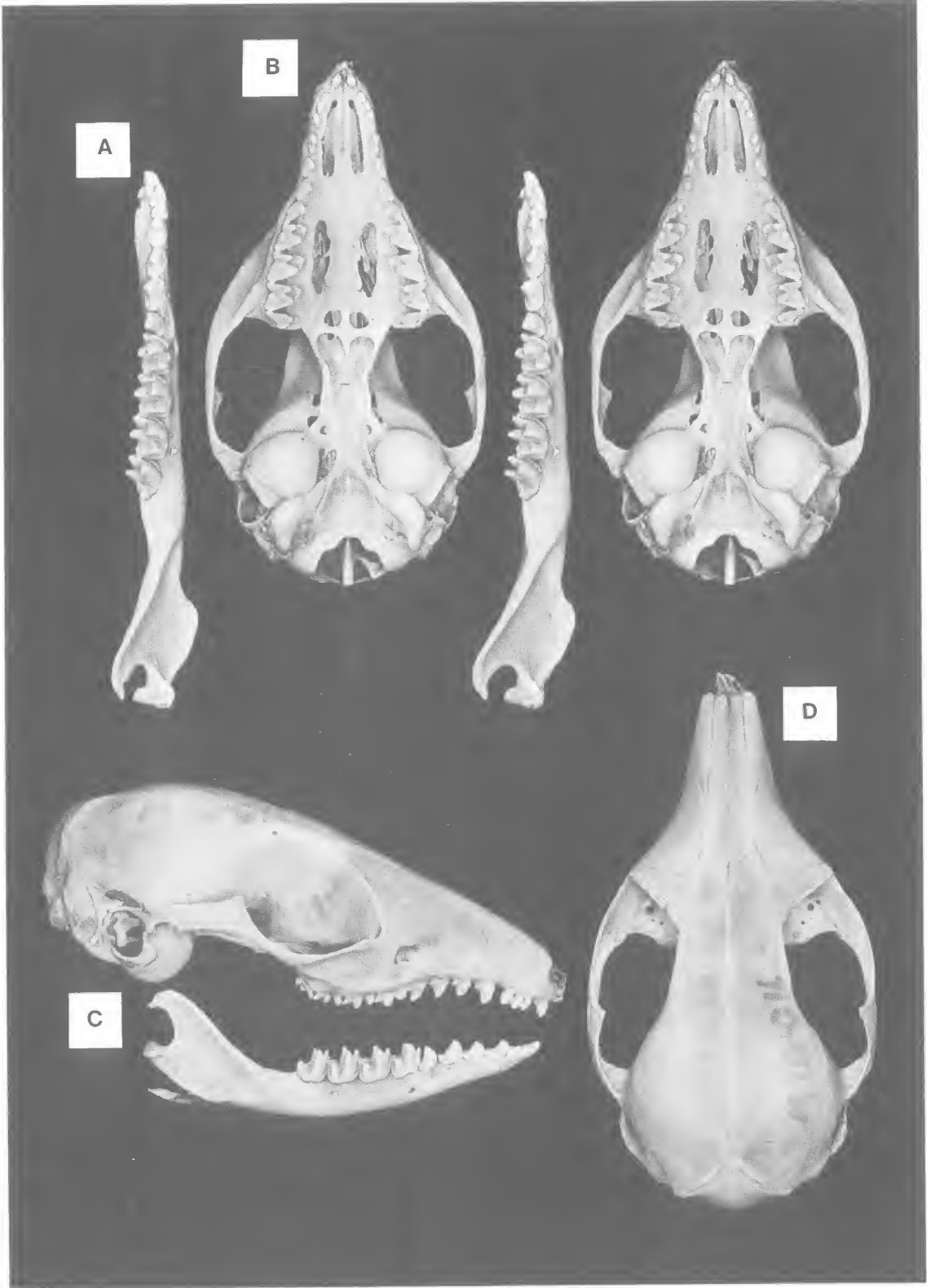


PLATE 10

Antechinomys laniger. A-D, JM819, adult, Tobermoray, N.T. A, \times 3.5. B-D, \times 2.9. E-G, JM820, adult, Tobermoray, N.T. E-G, \times 2.9.

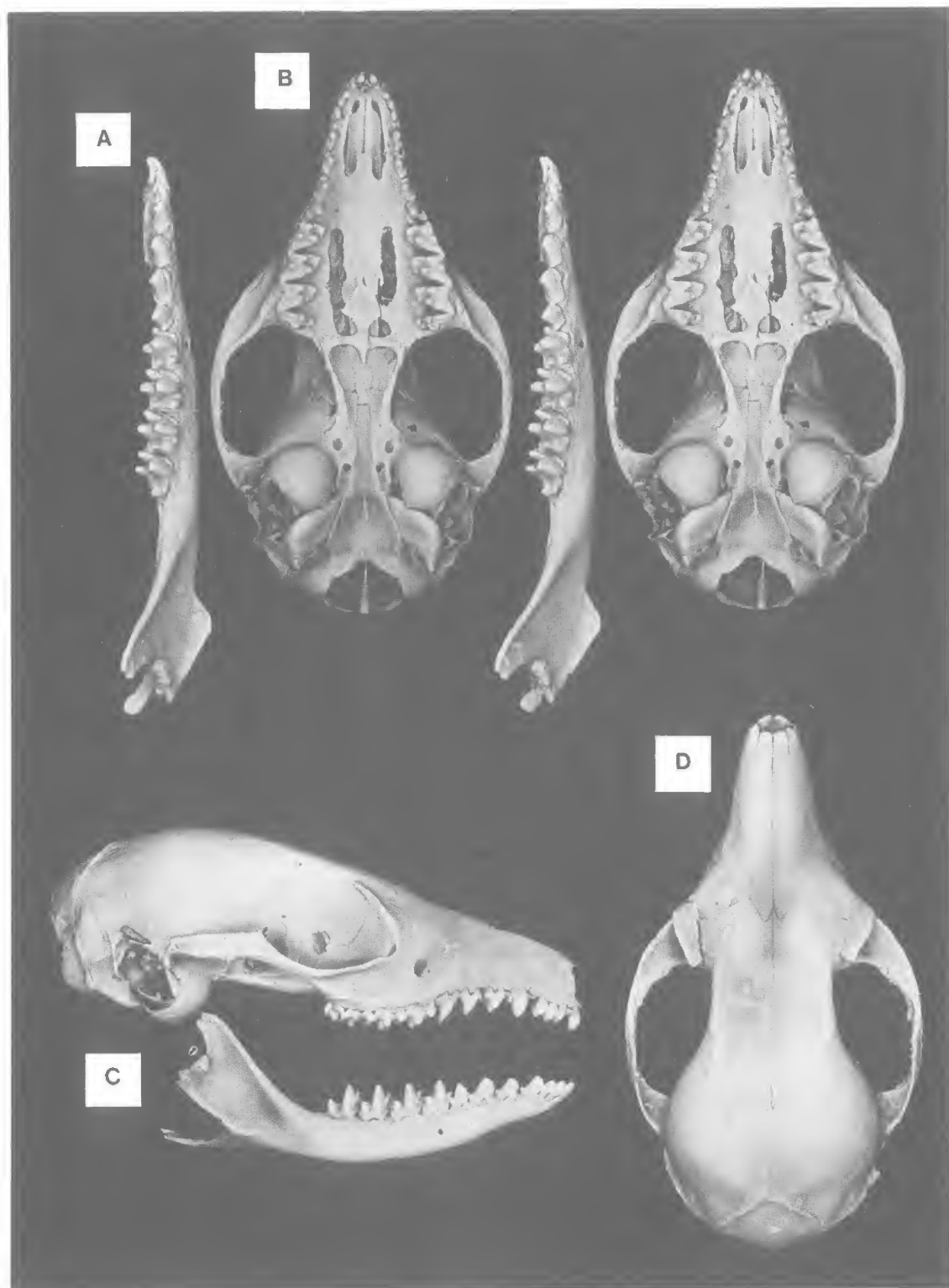


PLATE 11

A-D, *Antechinomys laniger* (*spenceri* form), WAM M5886, adult,
Warburton Range, W.A. A, E, $\times 4.0$. B, C, $\times 2.7$. D, $\times 3.0$.

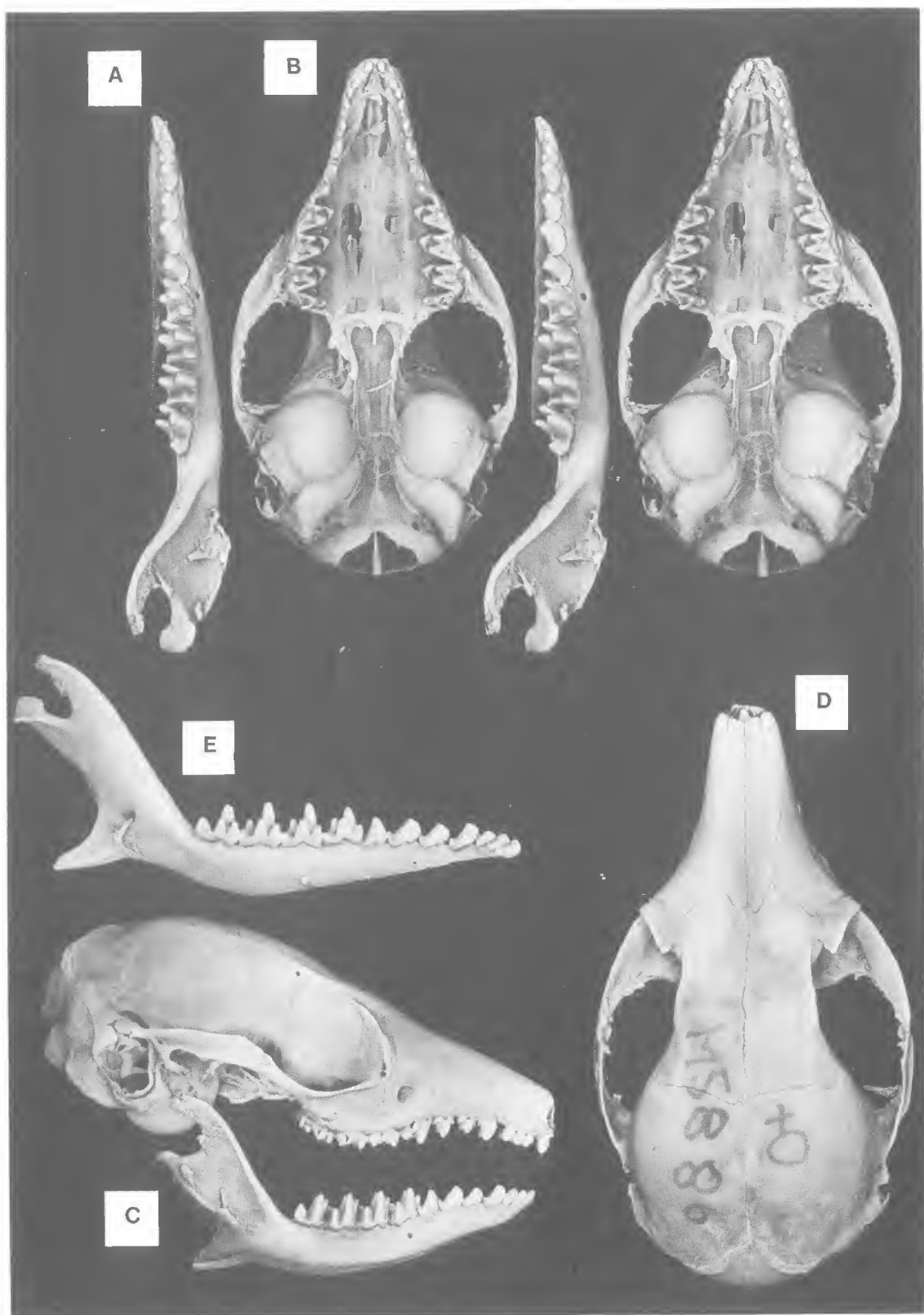


PLATE 12

A–D, *Antechinomys laniger*. A–C, BM1939.2997, adult, Cedar Bay, Qld, $\times 2.9$. D, scanning electron microscope photographs of *A. laniger* (*spenceri* form), WAM M2860, RI₁–M₄, approx. $\times 16$. E, as for D, approx. $\times 54$. Complex series of cusps and crests in region of entoconid described in text.

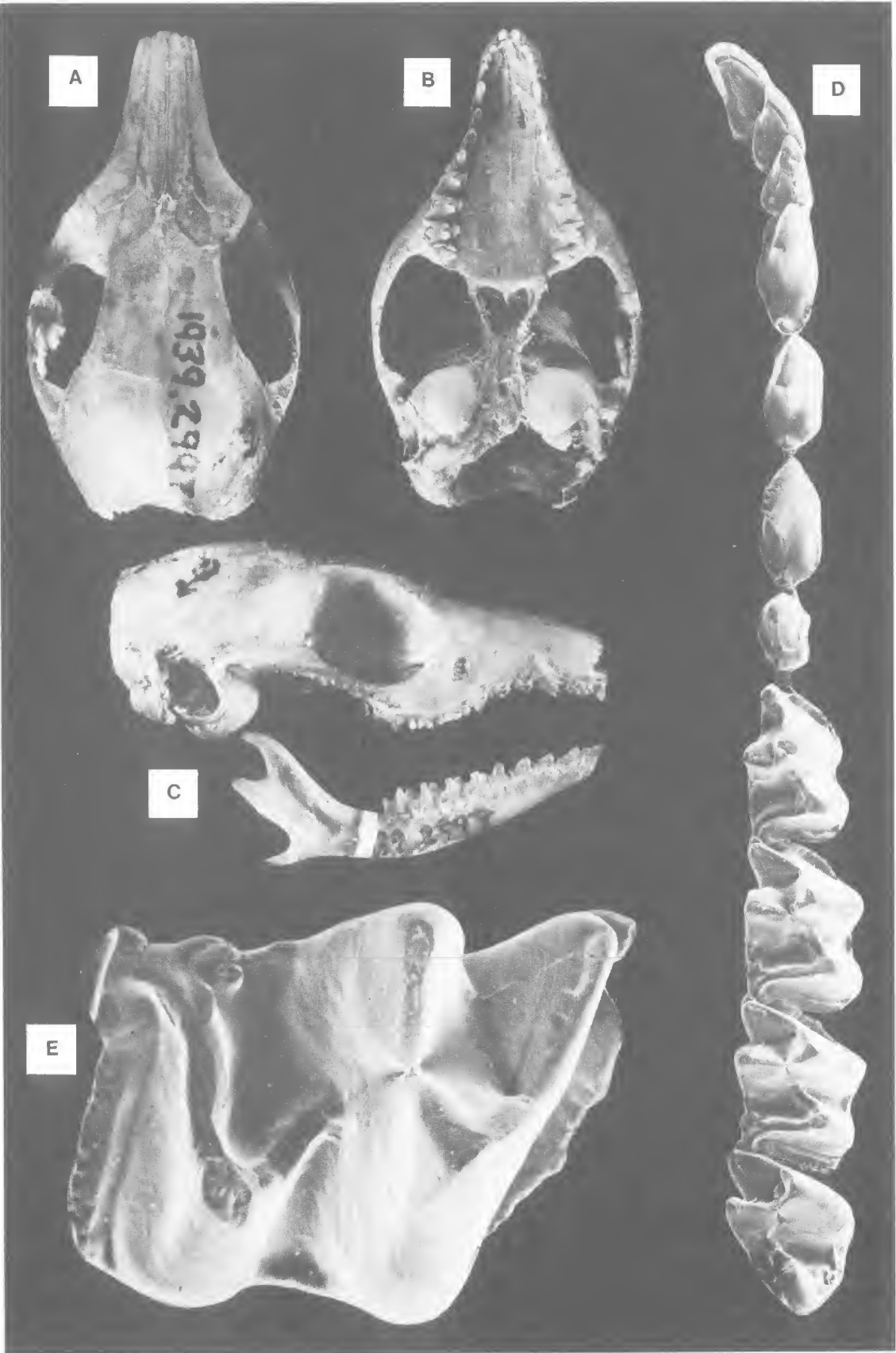
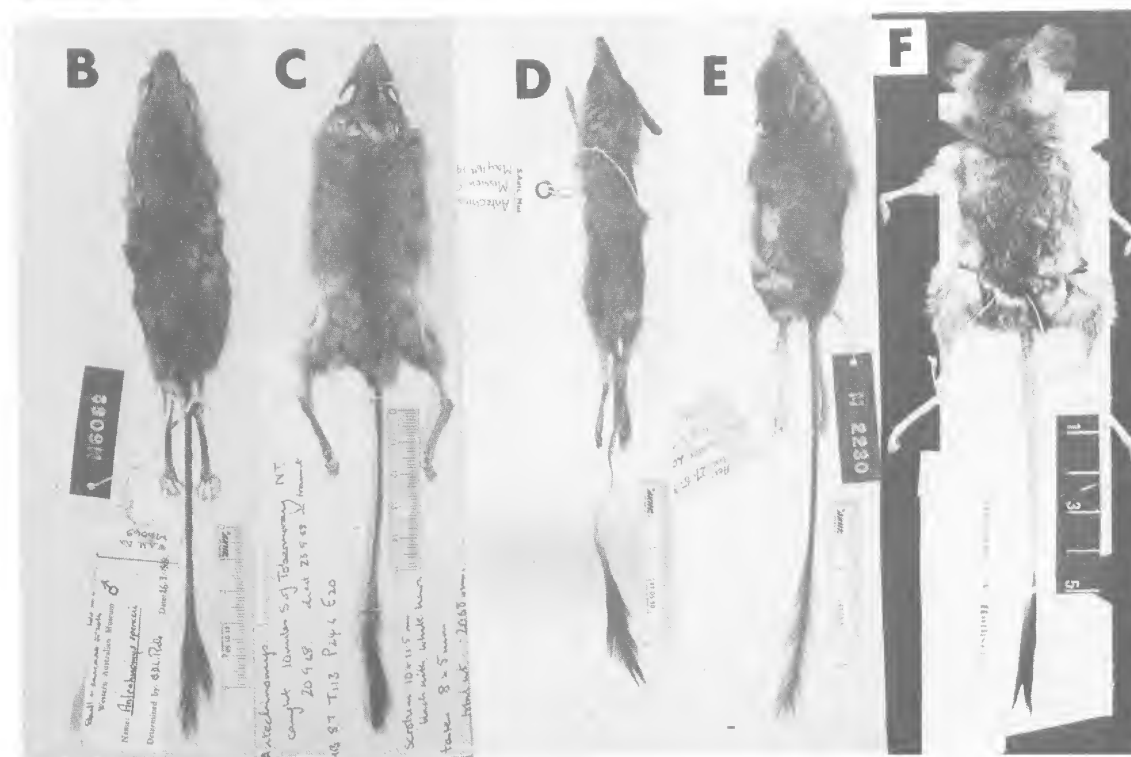


PLATE 13

A-F, *Antechinomys laniger*. A, *spenceri* form (photographs W. D. L. Ride). B, *spenceri* form, WAM M6069, Warburton Range, W.A. C, *laniger* form, JM819, Tobermoray, N.T. D, *laniger* form, SAM M857, Roper River, N.T. E, *laniger* form, WAM M2230, Lake Grace, W.A. F, *laniger* form, BM1939.2997, Cedar Bay, Qld.





KOOBOR NOTABILIS (DE VIS), AN UNUSUAL KOALA
FROM THE PLIOCENE CHINCHILLA SAND

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ABSTRACT

Koobor notabilis from the late Pliocene Chinchilla Sand of southeastern Queensland is known from a maxillary fragment (F691) with P^4 – M^3 , and an additional, referred P^4 (F8976). It represents a unique group of koala-like animals known also from the early Pliocene Allingham Formation of northeastern Queensland.

De Vis (1889) describes *Pseudochirus notabilis* (as *Pseudochirus ? notabilis*) from a maxillary fragment (F691) with P^4 – M^3 . He records the type locality in Queensland as (p. 105) '... a gathering place enriched by agencies of unusal [sic] range and efficacy ...'. Bartholomai (pers. comm. to Mahoney and Ride 1975) suggests from the preservation of the specimen that it probably comes from the Chinchilla Sand, considered by Bartholomai (1973) to be late Pliocene in age.

Archer in Archer and Wade (1976a) describes *Koobor jimbarratti* from the lower Pliocene Allingham Formation. Archer also refers *notabilis* to this genus, but notes differences between the Chinchilla Sand and Allingham species.

In the present work, a description of *K. notabilis* is given which supplements that of De Vis (1889) and an additional Chinchilla Sand specimen (F8976) is described.

Numbers prefixed by F are in the Queensland Museum fossil vertebrate collection. Numbers prefixed by UCMP are in the palaeontological collections of the University of California at Berkeley.

PHASCOLARCTIDAE OWEN
Koobor Archer

***Koobor notabilis* (De Vis, 1889)**
(Fig. 1; Plate 14)

Pseudochirus ? notabilis De Vis, 1889, p. 113–4.

HOLOTYPE: F691, left maxillary fragment with P^4 – M^3 , and anterior parts of alveoli for M^4 .

TYPE LOCALITY: Darling Downs, Queensland. Exact locality inadequately stated by De Vis, but Bartholomai (pers. comm. to Mahoney and Ride 1975) suggests the

possible provenance as the Chinchilla Sand of late Pliocene age on the basis of preservation. Matrix on the specimen consists of clay and rounded sand grains, a lithology common at Chinchilla, but uncommon on the eastern Darling Downs.

DIAGNOSIS: Differs from only other known species, *K. jimbarratti* in that parastyle less well-developed; preprotocrista does not intersect base of paracone; buccal basins better-developed; crown appears less wrinkled; crenulations contacting anterior cingulum better-developed; conules better-developed; and there are accessory lingual cusps on bases of hypocone or protocone.

DESCRIPTION OF HOLOTYPE: P^4 basically bicuspid, with posterior being slightly larger than anterior cusp. Both cusps conical joined at base. Two small crests radiate buccally from worn tip of posterior cusp and extend part way up its buccal flank. Buccal wall of anterior cusp damaged and no details preserved. Remnant of slight lingual crest extends lingually from worn tip of anterior cusp, up lingual face and contacts rudimentary lingual cingular swelling. Similar lingual crest may occur on posterior cusp but wear has obliterated any positive evidence. A short subhorizontal crest appears to extend anteriorly from tip of anterior cusp to broken anterior end of tooth. However, may also represent only broken edge of enamel. Large wear facets on tips of anterior and posterior cusps tilt towards one another and contact mesiolingually. Smaller wear facet developed on lingual cingular swelling. Mesial points of two sets of facets line up along an inclined transverse line, and represent an evidently large conical postero-buccally positioned cusp on P_4 serially homologous

premetacrista and postparacrista, leaving buccal opening to central basin. Opening of buccal paracone basin relatively more posterior in position than in M^1 , and whole basin less well-enclosed buccally. Relatively short postmetacrista results in less symmetrical and less well-enclosed buccal metacone basin. Point of inflection in poorly-defined ectoloph present between buccal ends of postparacrista and premetacrista. Slight suggestion of posterolingual paracone rib but perhaps indistinguishable from vertical crenulations. Very slight to absent paracone rib. Prehypocrista appears to terminate on posterobuccal flank of protocone. Postprotocrista appears less well-developed than in M^1 and may have even been absent. Preprotocrista extends anterobuccally directly to anterior cingulum without point of inflection. No basin formed between it and anterior cingulum. Protoconule worn but evidently small, and base connected to buccal side of preprotocrista as well as base of paracone. Anterior end did not reach anterior edge of tooth. Anterior and posterior cingula simple and comparable in morphology to posterior cingulum of M^1 . Crenulations less apparent over whole surface of tooth (perhaps due to wear) except on anterior flank of preparacrista, anterior cingulum, and protoconule.

M^3 as in M^2 except as follows: Preparacrista and premetacrista subequal in length, and longer than postparacrista which is longer than postmetacrista. Small anterior limb present on longitudinal crest at buccal end of postparacrista. Short postparacrista results in less symmetrical buccal paracone basin. Point of inflection in buccal outline of tooth broader than in M^2 and also encompasses buccal end of postparacrista. Small prominent cusp on posterolingual flank of protocone but none on anterolingual flank of hypocone.

M^4 suggested only by alveoli. These represent anterobuccal and lingual roots and indicate tooth was wider anteriorly than posterior half of M^3 .

Meristic gradients along tooth row from M^1 to M^3 as follows: Preparacrista becomes longer and extends further in buccal direction. Postparacrista M^1 shorter than that of M^2 which is longer than that of M^3 . Postparacrista extends less in buccal direction. Premetacrista M^1 shorter than that of M^2 which is longer than that of M^3 . Premetacrista extends less in buccal direction. Postmetacrista steadily decreases in length. Buccal paracone and metacone basins become less well-developed. Distance between buccal ends of postparacrista and premetacrista decrease M^1 to M^2 but increase M^2 to M^3 . Longitudinal buccal crests on postparacrista and postmetacrista decrease in development but on preparacrista and premetacrista increase in

development. Postprotocrista decreases in apparent significance. Protoconule decreases in size. Anterior cingulum becomes markedly more simple between M^1 and M^2 (M^3 as in M^2). Tooth width increases from M^1 to M^2 but decreases from M^2 to M^3 . Relative width of posterior part of tooth (line through hypocone and metacone) steadily decreases.

REFERRED SPECIMEN: F8976, collected in 1973 by screenwashing surface scree of a small knoll (Queensland Museum Locality no. L294) of the Main Gulley System, on the Chinchilla Rifle Range (Rifle Range No. 78, Parish of Chinchilla). The surface scree is an erosional remnant of the conglomerate forming the crest of the knoll at this point. The tooth appears to be an unworn right P^4 of *Koobor notabilis*. Although it is narrower than P^4 of the holotype, some variation might be expected in tooth width. It is basically similar in morphology to P^4 of the holotype.

Two median longitudinal crest units are present which, with wear, would appear as two cusps. Anterior crest unit has inclined anterior crest intersected near anterior end by small vertical crest. Posteriorly, near apex, anterior longitudinal crest crossed transversely by small crest which ascends buccal and lingual face. Longitudinal crest continues posteriorly, ending abruptly opposite posterior crest unit. On buccal base of anterior longitudinal crest, small but prominent cusp occurs. Posterior crest unit with longitudinal crest which passes posteriorly from apex to posterior end of tooth, then swings gracefully in lingual direction. Anteriorly from apex, short longitudinal crest extends towards anterior crest unit, intersected near anterior end by well-developed crenulated vertical buccal crest. Anterior tip of anterior longitudinal crest just passes buccal to posterior tip of anterior crest unit. Buccal flank of posterior crest unit with vertical crenulations. Steep-sided median transverse valley marks boundary between anterior and posterior crest units. Lingual base of crown mildly crenulated and could provide surface for wear facet in homologous position on P^4 of holotype.

Reference of this undoubted Chinchilla Sand specimen to *Koobor notabilis* adds credence to the suggestion of Bartholomai (noted above) that the holotype is also from the Chinchilla Sand.

DISCUSSION

It seems strange that De Vis's proclivity for naming new genera should have abandoned him at one of the few times such action was warranted. Whatever the reasons for De Vis's hesitancy, there

can be no doubt that *Koobor* is generically distinct from other known phascolaroids.

Koobor is diagnosed from all other phascolarctids by Archer in Archer and Wade (1976). The additional characters of F691 and F8976 permit further points of difference to be noted. *Koobor* differs from *Phascolarctos* most significantly in its markedly dissimilar P⁴ morphology; longer and narrower molars; and construction of the buccal paracone and metacone basins. *Koobor* differs from *Litokoala* (known only from M¹) in the significantly different construction of the buccal paracone and metacone basins, and the different buccal shape of the crown. *Koobor* similarly differs from *Perikoala* (paratype UCMP45343, Tedford and Woodburne 1967) in at least the construction of the buccal paracone and metacone basins.

Recognition of *Koobor* as a phascolarctid indicates the diversity and hence probable antiquity of the family. The P⁴ morphology of *Koobor* is one of the most distinctive characters of the genus. Combined with the unusual molar morphology, it suggests that the stock to which *Koobor* belongs diverged from that to which *Phascolarctos* belongs possibly as early as mid-Tertiary times. *Koobor notabilis* probably represents a late Tertiary survivor of a previously more diverse group.

P⁴ of *Phascolarctos* has a longitudinal crest which appears to be the homologue of both cusps on P⁴ of *Koobor*. In *Phascolarctos*, this crest shows a mild inflection and is buccally convex. Wear facets on this crest in *Phascolarctos* are in homologous positions with wear facets on the two cusps of P⁴ in *Koobor*. The anterior facet in *Phascolarctos* is produced by occlusion with a part of the longitudinal crest of P₄. The posterior facet is produced by occlusion with the posterobuccal cusp or crest of P₄. In *Koobor*, the steep angles of the wear facets and their proximity to one another

suggests P₄ has a large posterobuccal cusp. It is also possible that a second tall cusp or longitudinal crest occurred which closely approximated the posterobuccal cusp.

K. jimbarratti from the early Pliocene Allingham local fauna is known from only one tooth. It appears to represent essentially the same kind of animal as *K. notabilis*, but differs in enough minor details to warrant specific separation. It has been interpreted (Archer in Archer and Wade 1976) as being older and possibly structurally ancestral to *K. notabilis*.

ACKNOWLEDGMENTS

Mr Colin Limpus, Mr Norman McIntyre, Mr Bernard Cooke (Kelvin Grove Teachers College) and many student teachers helped in the recovery of Chinchilla specimens including F8976.

Dr Alan Bartholomai (Queensland Museum) kindly read a draft of this paper. Mr Alan Easton (Queensland Museum) took the light photographs, Mr John Hardy (University of Queensland) took the scanning electron microscope photograph.

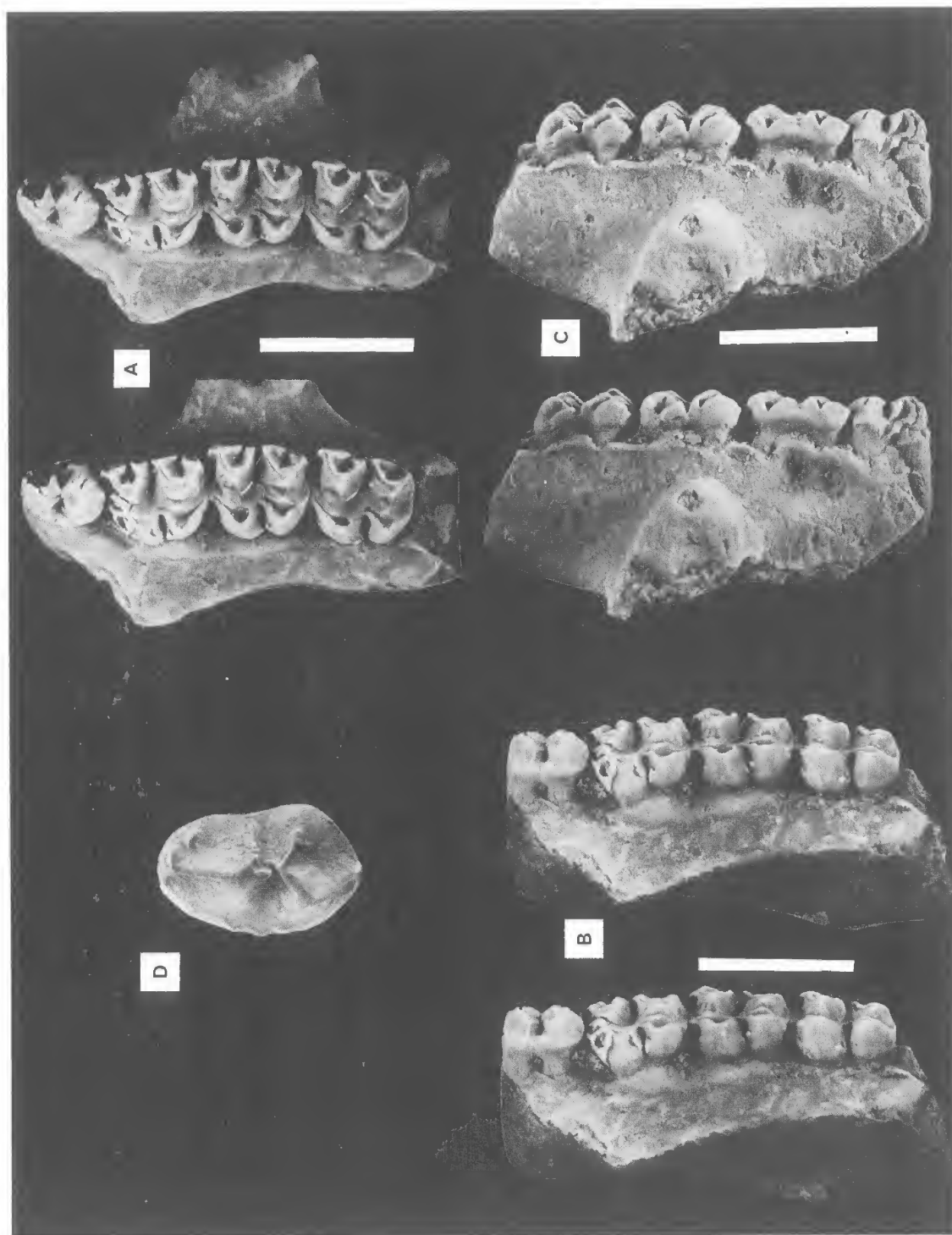
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PLATE 14

Koobor notabilis. A–C, stereopairs of holotype (F691) showing occlusal (A), lingual oblique (B), and buccal (C) views. D, scanning electron microphotograph of referred LP⁴ (F8976). Line represents one cm.





ORIGINS AND SUBFAMILIAL RELATIONSHIPS OF *DIPROTODON* (DIPROTODONTIDAE, MARSUPIALIA)

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ABSTRACT

The Pleistocene *Diprotodon* is shown to be similar in dental and cranial anatomy to the Pliocene *Euryzygoma*. Although sufficient characters indicate the generic distinction of the two kinds of diprotodontids, they are not regarded as distinctive enough to warrant subfamilial separation. Accordingly, all forms regarded previously as nototheriines are referred to the Diprotodontinae.

One of the enigmas of marsupial origins is the ancestry of the highly specialized *Diprotodon*. Species of this genus occur in Pleistocene deposits apparently without closely related ancestors in older deposits.

While examining large series of diprotodontid specimens from the late Pliocene Chinchilla Sand, it became apparent that dental variation in the nototheriine *Euryzygoma dunense* incorporated many of the characters otherwise thought to be diagnostic of *Diprotodon*.

Specimen numbers with an F prefix are from the Queensland Museum fossil vertebrate collections. A P prefix indicates a specimen from the palaeontological collections of the South Australian Museum.

DIAGNOSTIC CHARACTERS OF *DIPROTODON*

Stirton, Woodburne, and Plane (1967) diagnose the Diprotodontinae (which they regard as containing only *Diprotodon*) as follows: P⁴ small, quadritubercular, complex, lophodont, with 'horse-hoof' pattern, metacone and paracone distinct, protocone connected to metacone, no hypocone, small parastyle; P₄ bilophodont, lophs uniting with wear to form 'horse-hoof' pattern, paralophid reduced, with posterior cingulum; molars without midlinks, narrow deep transverse median valleys with cement; palate has deep groove between diastemal crests; no epitympanic fenestra in superficial meatus posterior to glenoid fossa; large postglenoid process. In addition, it is often noted (e.g. Marshall 1973) that teeth of *Diprotodon* have a characteristic punctate surface texture.

COMPARISON OF *DIPROTODON* AND *EURYZYGOMA*

P⁴: F3370 shows the common *Euryzygoma* condition of P⁴ with a distinct protocone connected to a wide parametacone by a protoloph. There is a marked swelling on the posterobuccal flank of the protocone, and on the postero-lingual flank of the parametacone. An alternative and less common condition is shown by F3367 where these swellings actually contact, thereby enclosing a central basin. Except for the parametacone, this is very similar to the *Diprotodon* condition and almost identical to one *Diprotodon* specimen (F6635). Although no *Euryzygoma* P⁴ observed has a separate paracone and metacone, the parametacone of some (e.g. F7972) is very wide and on its buccal flank a vertical groove suggests demarcation between a paracone and metacone. In any case, although in most unworn specimens of *Diprotodon* the paracone and metacone are distinct, they are frequently very close together, and joined by a high parametacone crest. In slightly worn specimens (e.g. F7971), the metacone and paracone are undifferentiable as the ends of the narrow parametacone crest. In *Euryzygoma*, as in *Diprotodon* a small parastyle is normally present (e.g. F8941) but sometimes is very small (e.g. F7973).

P₄: Comparison of P₄ in *Diprotodon* and *Euryzygoma* is limited because there are no lower premolars of *Euryzygoma* sufficiently unworn to clearly determine the crown pattern. P₄ of the holotype of *E. dunense* (F376) and F5972 give some indication of shape and suggest the tooth is not horse-hoof shaped as it is in some *Diprotodon* (e.g. P10559). In F8943, an isolated P₄ of *Diprotodon*,

there are basically two high transverse crests, the metalophid and hypolophid, which are barely connected by an antero-lingual ridge from the hypolophid. With wear this would produce the normal horse-hoof pattern of *Diprotodon*. The anterior crest or, metalophid is also the posterior wall of a solid triangular trigonid. This pattern is not markedly different from that of *Euryzygoma*. In F5972 there is a low hypolophid and a higher trigonid. The trigonid posterior wall is the metalophid. A small crest extends posteriorly from the lingual end of the metalophid towards the hypolophid, and if not homologous, is at least analogous to the lingual crest linking the meta- and hypolophids of *Diprotodon*. A specimen of *Diprotodon* illustrated by Owen (1877, pl. 124) shows a P_4 in which the linking crest extends postero-lingually from the metalophid as in *Euryzygoma*.

MOLARS: As in *Diprotodon*, the molars of *Euryzygoma* lack midlinks and have narrow, deep transverse median valleys. The molars and premolars normally have a punctate enamel surface made of many fine irregular vertical crenulations. No specimen of *Euryzygoma* has been observed with cement. Although it is not uncommon for specimens of *Diprotodon* (e.g. F6633) to lack cement, this may in part result from older specimens having had their cement removed by preparators.

SKULL: The cranial characters regarded by Stirton, Woodburne and Plane (1967) to diagnose diprotodontines are, as they note, also present in nototheriines. A skull of *Euryzygoma* from the Allingham Formation figured in Archer and Wade (1976) indicates that not all members of this genus had grossly enlarged zygomatic flanges, and such a structurally simple *Euryzygoma* could have been ancestral to *Diprotodon*.

DISCUSSION

Diprotodon is so far only recorded with certainty from Pleistocene deposits (Stirton, Woodburne and Plane 1967). Marshall (1973) lists it in the Fisherman's Cliff local fauna, regarded by him to be either late Pliocene or Pleistocene. This record is based only on a tooth fragment and is doubtful. Woods (1962) records *Diprotodon* from the late

Pliocene (Bartholomai 1972) Chinchilla Sand. This record is probably based on one or more of the *Diprotodon*-like P^4 specimens described above. *Euryzygoma* is so far only recorded from the Chinchilla Sand and the older Allingham Formation (Archer and Wade 1976). There is thus no overlap between species of *Diprotodon* and *Euryzygoma*.

Morphological evidence presented above suggests that variation present in *Euryzygoma* foreshadows that of *Diprotodon*. The differences species of *Diprotodon* show from those of *Euryzygoma*, including the much larger size, higher-crowned teeth, distinct P^4 para- and metacones, and details of skull and post-cranial morphology, although clearly indicative of different genera, are probably not indicative of different subfamilies. The view proposed here is that *Euryzygoma* be regarded as structurally ancestral to *Diprotodon*, and that *Diprotodon*, *Euryzygoma*, and all other genera regarded by Stirton, Tedford and Plane (1967) to be nototheriines, be regarded as diprotodontines.

ACKNOWLEDGMENTS

Dr Alan Bartholomai (Queensland Museum) kindly read and commented on the manuscript. Mr Alan Easton (Queensland Museum) took the photographs.

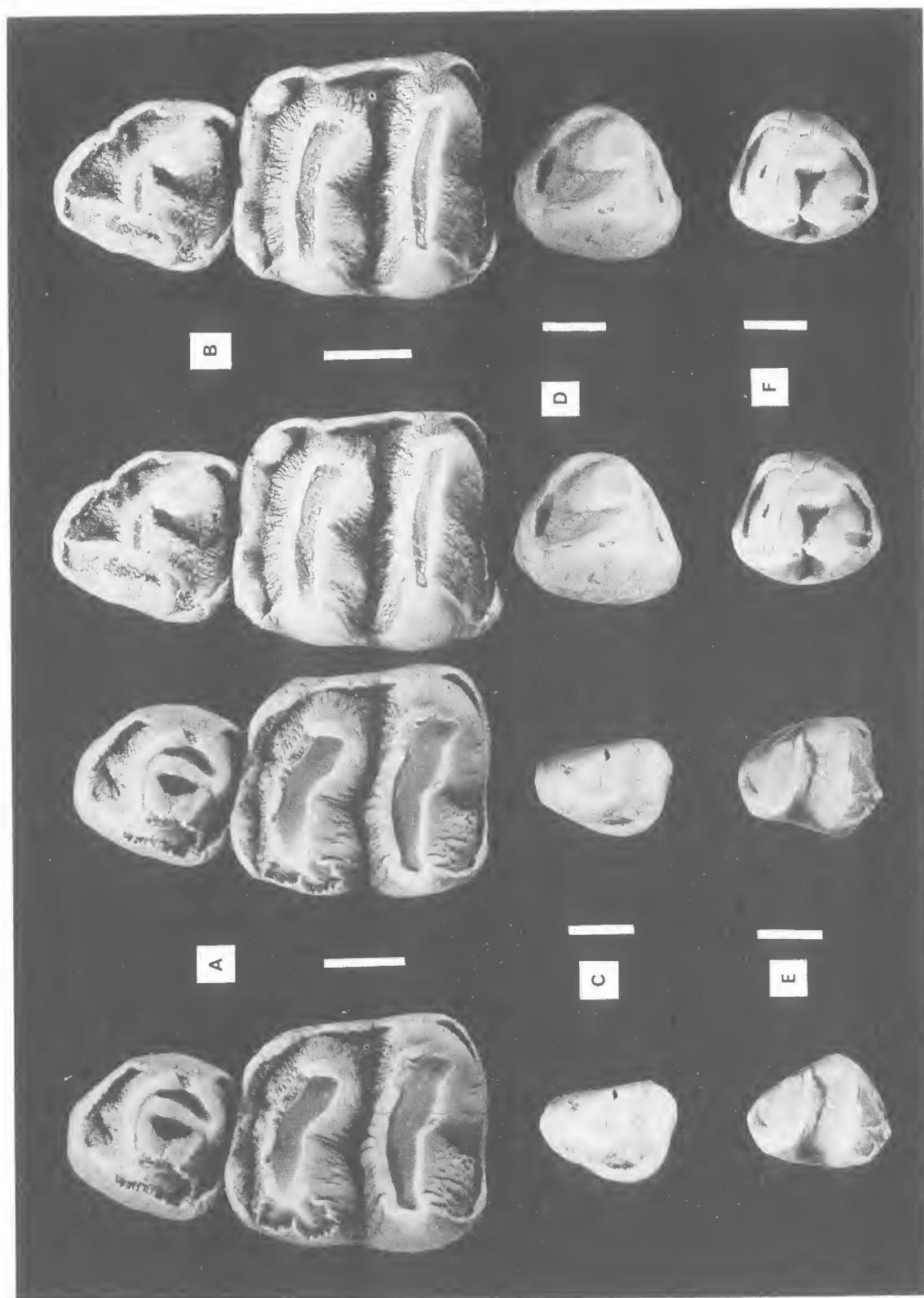
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PLATE 15

A–B, stereopairs of *Euryzygoma dunense* from Chinchilla Sand showing normal (B, F3370) and *Diprotodon*-like (A, F3367) configuration of P^4 morphology. C–D, stereopairs of *E. dunense* P_4 (C, F5966), and P^4 (D, F7972) showing incipiently bicuspid parametacone crest. E–F, stereopairs of *Diprotodon australis* from eastern Darling Downs deposits, P_4 (E, F8943) and P^4 (F, F6635) showing approximated para- and metacones, a homologue of the *Euryzygoma* parametacone crest. Line represents one cm.





THE FOSSIL VERTEBRATE FAUNA FROM PLEISTOCENE DEPOSITS AT CEMENT MILLS, GORE, SOUTHEASTERN QUEENSLAND

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ABSTRACT

The fossil fauna from the cave and fissure-fill deposits at Cement Mills, Gore, southeastern Queensland is identified and shown to comprise 31 taxa, all but three of which are marsupial. Macropodids represent the most abundant remains preserved. Eighteen of the species are extinct and several others may ultimately prove new. With the exception of one of the extinct forms, the material permits reasonable correlation of the deposits with other Australian Pleistocene sediments, although some Late Pleistocene or Recent deposition is suggested by the large representation of extant species. The deposits are believed to have accumulated by a combination of marsupial predators and wash and fill processes.

Fossil vertebrate remains were first recorded from the cave and fissure-fill deposits at Cement Mills, Gore, southeastern Queensland, by Longman (1945). At that time, nine species, including a rodent and a bird, were noted in the fauna. Subsequently, the Queensland Museum has undertaken field work on the deposits on a number of occasions, resulting in a substantial increase in knowledge of the fauna. Aspects of the occurrence and various elements of the Cement Mills fauna have been described and discussed in a number of studies by Woods (1960) and Bartholomai (1963, 1968, 1970, 1971b).

The deposits occur in restricted limestone developments within the Palaeozoic rocks of the New England Fold Belt. Siemon (1973) indicates that the limestones quarried at Cement Mills form part of the Texas Beds of ?Upper Devonian to ?Upper Carboniferous age. These Beds comprise an intensely deformed sequence of 'flysch-like, regularly interbedded lithic sandstones and mudstones, with minor chert, jasper, intraformational conglomerate, intermediate volcanics, and limestone containing Viséan corals'.

The fossil vertebrates occur sporadically where the cave earths have been intersected by the quarrying operations. Most are firmly cemented within the compact sediment, but it is apparent from the state of preservation of some of the earlier collections, that considerable material has come from essentially unconsolidated cave earths. Examination of the fossil deposits *in situ* has not

succeeded in establishing any stratification within available cave earth sections.

A full discussion of the Cement Mills fauna is felt desirable to provide a basis for studies of other cave faunas in southeastern Queensland and eastern Australia generally.

Measurements throughout are in millimetres.

THE CEMENT MILLS FAUNA

REPTILIA

Family SCINCIDAE

Tiliqua scincoides (Shaw, 1790) (Plate 16, fig. 1)

The Blue-tongue Lizard, *T. scincoides*, is known from a single specimen, F7709, a partial left dentary. The individual from which this was derived was relatively large. Longman (1945) erroneously identified this specimen as resembling *Trachysaurus rugosus*, another of the large scincid lizards.

AVES

Family MEGAPODIIDAE

Progora naracoortensis van Tets, 1974

Only one bird fossil, F2769, has as yet been recovered from the Cement Mills deposits. This was originally identified by Longman (1945) as the Scrub Turkey, *Alectura lathami*, but has been reassessed by van Tets (1974) as *Progora naracoortensis*.

TABLE I: MANDIBULAR MEASUREMENTS—CEMENT MILLS FAUNA

Material	P ₁	P ₂	DP ₃	P ₃	M ₁	M ₂	M ₃	M ₄
<i>Sarcophilus laniarius</i>								
F3734	—	—	—	—	—	12.8 × 8.6	14.0 × 9.1	—
F3706	—	—	—	—	—	11.5 × 7.6	13.7 × 8.5	—
F3725	—	—	—	—	—	13.2 × —	15.0 × 9.3	16.9 × 8.8
F3726	—	—	—	—	—	11.9 × 7.8	—	—
F3708	—	7.6 × 7.3	—	7.7 × 6.0	10.0 × 6.8	—	—	—
F2771	—	—	—	—	—	—	12.9 × 7.9	13.9 × 8.1
F3705	—	—	—	6.6 × 6.7	10.6 × 7.0	12.0 × 7.6	14.3 × 7.9	13.3 × 7.2
F3704	—	—	—	—	9.8 × 6.6	11.2 × 7.2	12.2 × 7.3	13.4 × 6.8
F3733	—	—	—	—	10.3 × 7.3	—	—	—
<i>Thylacinus cynocephalus</i>								
F3737	—	10.2 × 4.2	—	—	—	—	—	—
F7345	—	—	—	—	—	—	—	16.4 × —
<i>Thylacoleo carnifex</i>								
F5708	—	—	—	39.7 × 14.1	—	—	—	—
F7341	—	—	—	—	15.1 × 10.3	—	—	—
<i>Vombatus ursinus</i>								
F2774	—	—	—	6.4 × 5.0	10.7 × 6.0	11.2 × 6.8	— × 6.9	—
F7364	—	—	—	6.8 × 4.8	10.9 × 6.2	11.9 × 6.4	12.2 × 7.5	—
F7348	—	—	—	—	9.6 × —	—	—	—
F7349	—	—	—	6.0 × 5.4	11.2 × 5.5	12.0 × 6.5	—	—
<i>Phascodon gigas</i>								
F2772	—	—	—	18.3 × 12.0	22.7 × 13.8	24.1 × 14.2	—	—
*F7350	—	—	—	12.9 × 8.7	22.5 × 12.0	—	—	—
<i>Phascodon cf. P. magnus</i>								
F7351	—	—	—	—	—	—	17.8 × 12.3	—
F7352	—	—	—	—	19.3 × 10.6	—	—	—
<i>Potorous aff. P. tridactylus</i>								
F6092	—	3.5 × 2.0	3.3 × 1.8	5.2 × 2.1	3.8 × 2.6	4.2 × 3.3	4.1 × 3.3	—
F6093 (rt.)	—	—	—	5.6 × 2.2	3.6 × 2.6	—	—	—
F6093 (lt.)	—	—	—	5.8 × 2.2	3.7 × 2.5	—	—	—
<i>Bettongia</i> sp.								
F6134	—	—	—	6.5 × 2.1	4.1 × 2.9	4.3 × 3.6	3.6 × 3.4	3.1 × 2.8
<i>Protemnodon anak</i>								
F7639	—	7.7 × 3.9	—	12.3 × —	9.0 × 5.7	—	—	—
F7641	—	7.6 × 4.0	9.1 × 4.9	—	9.7 × 6.0	—	—	—
<i>Protemnodon brehus</i>								
F7338	—	—	—	—	—	—	—	19.0 × 13.0
<i>Protemnodon roechus</i>								
F7336	—	—	—	— × 5.6	—	14.2 × —	17.5 × —	18.1 × 11.8

MAMMALIA

Superorder MARSUPIALIA

Family DASYURIDAE

Dasyurus aff. **D. viverrinus** (Shaw, 1800)
(Plate 16, fig. 4)

The only specimen of *Dasyurus* to have been recovered from the deposits, F3703, was considered by Bartholomai (1971b) who concluded that although no teeth are preserved, 'proportions of the ramus and its morphology suggest that it is ... most likely of *D. viverrinus*'.

Sarcophilus lanarius (Owen, 1838)
(Plate 16, fig. 3)

S. lanarius is represented in the Cement Mills fauna by a relatively large sample comprising a partial skull, three maxillary specimens, 10 mandibular rami and 19 isolated teeth. No morphological differences are evident between this sample and material from the Pleistocene fluvial deposits of the Darling Downs area, southeastern Queensland and elsewhere. Longman (1945) recognised the presence of this species in the deposit. Measurements are presented in Tables 1 and 2.

Family THYLACINIDAE

Thylacinus cynocephalus (Harris, 1808)
(Plate 16, fig. 7)

Two specimens of *T. cynocephalus* are present in the fauna, F3737, a partial right ramus with P₂ and P₃ broken, and F7345, an isolated right M₄. The posterior cingulum in P₂ is very reduced compared with material from other Pleistocene deposits but M₄ is morphologically identical with recent material used for comparison. Measurements presented in Table 1 fall within the range for recent material listed by Ride (1964), but slightly outside that for Eucla Division fossil thylacines from Western Australian caves (Lowry, 1972).

Family PERAMELIDAE

Isodon sp.
(Plate 16, fig. 12)

The Short-nosed Bandicoots are represented by only two fragmentary specimens, one of which, F7847, a partial left ramus, lacks teeth. The other, F2773, a partial left maxilla with M¹-M³, was mentioned by Longman (1945) as *I. obesulus*. While this specimen is undoubtedly referable to *Isodon* on morphological grounds, it is smaller than any modern specimens in the collections of the Queensland Museum. It is possible that it may prove distinct when a better and more complete sample is available. Its measurements are listed in Table 2.

Perameles nasuta Geoffroy, 1804
(Plate 16, fig. 6)

A reasonably large sample of *P. nasuta* is present in the Cement Mills collection, comprising three partial crania, two maxillae, 24 partial rami and three isolated molars. The majority of specimens represent juvenile individuals. Slight differences are evident between the fossil and extant samples of *P. nasuta*. In particular, the premolars appear less well-developed in the Cement Mills sample, while the canine also appears to be consistently smaller in similarly aged specimens. The differences do not appear sufficient to warrant separation of the Cement Mills material. Summaries of measurements appear in Table 3, while those for recent material are listed in Table 4.

Family PHASCOLARCTIDAE

Phascolarctos stirtoni Bartholomai, 1968

Bartholomai (1968) described this fossil koala from the Cement Mills deposits, distinguishing it from living koalas by a number of features including its much larger size and stronger accessory ridging in upper molars.

Family THYLACOLEONIDAE

Thylacoleo carnifex Owen, 1859

A reasonably large sample of *T. carnifex* is present in the Cement Mills fauna, suggesting that the caves and fissures may have provided lairs for this extinct animal. Differences between the present sample and that from the Pleistocene fluvial deposits of the eastern Darling Downs are minor, P₃ being slightly less convex labially in occlusal view. This is interpreted as intraspecific variation. Longman (1945) noted the presence of this species in the fauna. Four mandibular and five maxillary fragments are represented. Measurements for this sample appear in Tables 1 and 2.

Family VOMBATIDAE

Vombatus ursinus (Shaw, 1800)
(Plate 16, fig. 9)

V. ursinus is represented by five specimens, four of which are mandibular. The sample is morphologically inseparable from modern material, although the ramus in one of them, F7346, is slightly deeper than in the available extant sample. This is not, however, considered significant. Measurements are provided in Tables 1 and 2.

Phascolonus gigas (Owen, 1859)
(Plate 16, fig. 13)

A partial right ramus, F2772, is referred to *P. gigas*. All teeth present are broken, but sufficient

TABLE 3: SUMMARY OF MEASUREMENTS FOR *Perameles nasuta* GEOFFROY, 1804 (FOSSIL)

Character	Maxillae					Mandible				
	n	X	O.R.	s	V	n	X	O.R.	s	V
P ₁ length	2	2.75	2.7-2.8	0.07	2.57	2	2.7	2.6-2.8	0.14	5.24
width posteriorly	2	0.8	—	—	—	2	0.7	—	—	—
P ₂ length	5	2.76	2.6-2.9	0.11	4.13	5	3.10	3.0-3.4	0.17	5.59
width posteriorly	5	1.04	1.0-1.1	0.05	5.27	5	0.94	0.8-1.0	0.09	9.52
P ₃ length	3	3.13	3.0-3.2	0.12	3.69	8	3.24	3.0-3.5	0.18	5.70
Width posteriorly	3	1.70	1.6-1.8	0.10	5.88	8	1.11	1.0-1.3	0.10	8.91
M ₁ length	6	4.02	3.8-4.3	0.20	5.08	10	3.50	3.3-3.8	0.16	4.47
width protoloph (-id)	6	2.53	2.5-2.7	0.12	4.78	9	1.69	1.5-2.0	0.14	8.08
M ₂ length	6	3.65	3.4-3.9	0.18	4.82	13	3.68	3.5-4.0	0.18	4.86
width protoloph (-id)	6	3.13	3.0-3.2	0.08	2.61	10	1.93	1.8-2.1	0.08	4.27
M ₃ length	7	3.70	3.5-4.0	0.16	4.41	15	3.75	3.4-4.1	0.19	5.12
width protoloph (-id)	7	3.51	3.4-3.7	0.11	3.04	15	2.01	1.9-2.1	0.06	3.18
M ₄ length	2	3.35	3.3-3.4	0.07	2.11	7	2.79	3.5-4.0	0.20	5.16
width protoloph (-id)	2	3.7	—	—	—	7	1.79	1.7-1.9	0.09	5.04

TABLE 4: SUMMARY OF MEASUREMENTS FOR *Perameles nasuta* GEOFFROY, 1804 (MODERN)

Character	Maxillae					Mandible				
	n	X	O.R.	s	V	n	X	O.R.	s	V
P ₁ length	20	2.89	2.5-3.4	0.21	7.22	23	3.09	2.6-3.4	0.18	5.76
width posteriorly	20	1.04	1.0-1.2	0.07	6.48	23	0.93	0.7-1.1	0.09	10.00
P ₂ length	24	2.90	2.5-3.3	0.18	6.23	23	3.40	3.1-3.8	0.16	4.56
width posteriorly	24	1.26	1.0-1.7	0.17	13.45	23	1.20	1.0-1.4	0.09	7.76
P ₃ length	22	3.34	2.6-3.9	0.38	11.46	23	3.67	2.9-4.1	0.36	9.86
width posteriorly	22	1.70	1.4-2.3	0.23	13.71	23	1.42	1.2-1.6	0.13	8.99
M ₁ length	20	4.07	3.6-4.4	0.21	5.05	23	3.52	3.1-3.9	0.21	5.98
width protoloph (-id)	20	2.88	2.6-3.8	0.31	10.82	23	1.96	1.6-2.2	0.14	7.20
M ₂ length	20	4.06	3.6-4.4	0.22	5.40	24	3.93	3.4-4.2	0.19	4.89
width protoloph (-id)	20	3.40	3.0-3.9	0.28	8.30	24	2.26	1.9-2.4	0.14	6.36
M ₃ length	20	4.32	4.0-4.6	0.23	5.28	23	4.07	3.6-4.4	0.18	4.52
width protoloph (-id)	20	3.84	3.5-4.6	0.33	8.47	23	2.36	1.9-2.6	0.16	6.60
M ₄ length	22	3.63	2.7-4.6	0.36	9.93	22	4.29	3.4-4.8	0.33	7.66
width protoloph (-id)	22	3.71	3.1-4.3	0.39	10.52	22	2.20	1.8-2.4	0.14	6.58

remains for confident reference of the specimen. Longman (1945) also considered this specimen to be *P. gigas*. P₃ possesses well defined, mesial vertical grooves on its labial and lingual surfaces and is relatively elongate compared with the length of M₁.

A second specimen, F7350, while having M₁ similar in size and morphology to that in *P. gigas*, has a comparatively shallower ramus and a much shorter P₃. While these characters may represent extreme variation within *P. gigas*, the specimen may be related to *P. lemleyi* Archer, from the lower Pliocene Allingham Formation (Archer and Wade, 1976). Measurements for both specimens are presented in Table 1.

Phascolomis cf. *P. magnus* Owen, 1872

(Plate 16, fig. 2)

This form is known only from two isolated molars in the Cement Mills collection. Identification has been made on size alone, the specimens being intermediate to molars in *P. medius* Owen and *P. gigas*. Measurements appear in Table 1.

Family DIPROTODONTIDAE Subfamily PALORCHESTINAE

Palorchestes azael Owen, 1874

(Plate 16, fig. 10)

An isolated left P₃, F3836, is referable to *P. azael*. It compares well with material from the

Pleistocene fluviatile deposits of the eastern Darling Downs, except that the posterior ridge from the parastyle is stronger in the Cement Mills specimen and there is no evidence of the presence of a labial cingulum. These differences are considered to represent intraspecific variation. Measurements appear in Table 2.

Palorchestes cf. *P. parvus* De Vis, 1895
(Plate 16, fig. 8)

A partial right maxilla, F7340, with M^1 – M^2 , compares reasonably well with specimens of *P. parvus* from the Chinchilla Sand, of Late Pliocene age. The specimen possesses very strong double linking across the median valley of M^1 , while the vertical ridges on the posterior metaloph surface differ in strength, that from the hypocone being much better developed. All links in M^2 are single. In size, the specimen is similar to *P. parvus*, listed by Woods (1958), and its measurements are provided in Table 2.

Subfamily NOTOTHERIINAE

Nototherium inerme Owen, 1845
(Plate 16, fig. 4)

The largest diprotodontid present in the deposits, *N. inerme* is represented by F7339, a posterior one-half of M_4 . This shows no wear on the lophid, but has a well-developed root, suggesting that it came from a sub-adult animal.

?Subfamily ZYGOMATURINAE

Two isolated incisors although diprotodontid, cannot be referred with certainty because of lack of comparative material in Upper Cainozoic collections of the Queensland Museum. These specimens, F7343 and F7344, represent right and left I^2 respectively, both of which are small compared with worn examples of this tooth in the available *Zygomaturus trilobus* sample. They differ much more, however, from other Upper Cainozoic diprotodontid genera, and are clearly not referable to *Nototherium*, the other large diprotodontid in the Cement Mills fauna.

Family MACROPODIDAE
Subfamily POTOROINAE

Potorous aff. *P. tridactylus* (Kerr, 1792)
(Plate 17, fig. 1)

Material here referred to *Potorous* aff. *P. tridactylus* comprises F6092, a juvenile right ramus with I_1 , P_2 – M_3 , P_3 excavated, F6093, associated rami with broken I_1 , P_3 – M_1 , and F6094, an adult maxilla with M^2 – M^4 . The sample illustrates comparable upward phalangerine curvature of I_1 , and

basically similar premolar and molar structure to that in living *P. tridactylus*, but the molars are somewhat more quadrate. The fossils are all relatively small, falling slightly outside the smallest observations in living *P. tridactylus* in the Queensland Museum collections. They are within the range of the New South Wales sample in the Australian Museum, Sydney. In view of the common occurrence of M_5 in potoroos, the maxillary fossil may contain M^3 – M^5 rather than M^2 – M^4 , although molar reduction and zygomatic arch position suggest the latter interpretation is correct. If so, M^4 is very reduced compared with *P. tridactylus* and is more comparable with that in living *P. gilberti* now regarded by Ride (1970) as a western form of *P. tridactylus*. Measurements for the sample are provided in Tables 1 and 2.

Aepyprymnus rufescens (Gray, 1837)
(Plate 16, fig. 11)

A large sample of *A. rufescens* has been recovered from the Cement Mills deposits and comprises five partial skulls, three partial maxillae, eight partial rami and six isolated teeth. Summaries of measurements for this sample are presented in Table 5, while those for living *A. rufescens* appear in Table 6. No significant size differences occur between the samples, the greatest C.D. being 0.71 in M^4 length.

The deciduous upper premolar is considered by Tate (1948) to possess five or six grooves, while P^3 is stated to have seven or eight grooves. The extant sample considered here agrees with the number of grooves indicated for P^2 , but five are more commonly present (92%, $n=24$). Number of grooves for P^3 ranges from six to nine, with seven being most common (72%, $n=43$). The fossil sample is slightly more variably in grooving of P^3 but not of P^2 . In P^3 , the range is from five to nine grooves. Lower premolars in fossil and recent samples agree well in variation in groove count.

The Cement Mills sample has been compared also with a small sample of fossil *Aepyprymnus* from the eastern Darling Downs and no differences are apparent.

Bettongia sp.
(Plate 17, fig. 8)

A partial right ramus, F6134, with P_3 – M_4 , has been recovered from the deposits. Because of its small size (see Table 1) specific status may be warranted when more material becomes available. The posterior cheek teeth are very small, P_3 is offset from the general line of the cheek teeth and its crest approximately parallels the lower enamel margin of the tooth; seven intermediary ridges are present

TABLE 5: SUMMARY OF MEASUREMENTS FOR *Aepyprymnus rufescens* (GRAY, 1837), CEMENT MILLS SAMPLE

Character	Maxillae					Mandibles				
	n	X	O.R.	s	V	n	X	O.R.	s	V
P ₂ length	3	7.0	6.5-7.6	0.55	7.89	4	6.4	5.7-7.0	0.59	9.24
width posteriorly	3	3.5	3.4-3.5	0.07	2.02	4	3.1	2.9-3.4	0.26	8.53
DP ₃ length	4	5.3	5.1-5.7	0.29	5.45	3	5.3	5.1-5.4	0.17	3.27
width protoloph (-id)	4	3.7	3.5-3.9	0.21	5.62	3	3.2	3.0-3.4	0.21	6.57
P ₃ length	9	9.4	8.5-10.9	0.78	8.33	6	8.9	8.6-9.5	0.32	3.62
width posteriorly	5	3.4	3.3-3.7	0.17	4.88	5	3.4	3.3-3.5	0.07	2.08
M ₁ length	9	5.5	5.0-5.9	0.28	5.10	6	5.5	4.7-5.9	0.41	7.54
width protoloph (-id)	8	4.6	4.4-4.8	0.15	3.28	6	3.8	3.4-4.1	0.26	6.86
M ₂ length	10	6.3	5.6-6.9	0.47	7.50	4	6.5	5.9-6.9	0.46	7.14
width protoloph (-id)	9	5.0	4.6-5.4	0.32	6.48	4	4.6	4.4-4.7	0.15	3.32
M ₃ length	10	6.5	6.0-7.1	0.34	5.20	5	7.1	6.5-7.6	0.49	6.86
width protoloph (-id)	10	5.0	4.8-5.2	0.11	2.11	4	5.2	5.1-5.4	0.15	2.93
M ₄ length	7	5.5	4.7-6.4	0.65	11.83	—	—	—	—	—
width protoloph (-id)	4	4.0	3.6-4.9	0.62	15.49	—	—	—	—	—

TABLE 6: SUMMARY OF MEASUREMENTS FOR *Aepyprymnus rufescens* (GRAY, 1837), RECENT SAMPLE

Character	Maxillae					Mandibles				
	n	X	O.R.	s	V	n	X	O.R.	s	V
P ₂ length	10	7.1	6.7-7.8	0.32	4.48	10	6.3	5.6-6.6	0.28	4.52
width posteriorly	10	3.2	2.9-3.5	0.18	5.51	10	3.0	2.8-3.2	0.13	4.44
DP ₃ length	10	5.7	5.5-5.9	0.15	2.63	10	5.2	4.5-5.6	0.32	6.08
width protoloph (-id)	10	3.7	3.4-3.9	0.17	4.51	10	2.8	2.5-3.0	0.18	6.30
P ₃ length	16	9.5	9.0-10.1	0.32	3.41	16	8.5	7.8-9.4	0.40	4.71
width posteriorly	16	3.5	3.1-4.1	0.25	7.20	16	3.2	2.9-3.5	0.17	5.47
M ₁ length	22	5.8	5.0-6.4	0.41	7.00	19	5.3	4.6-6.2	0.38	7.21
width protoloph (-id)	22	4.3	3.9-4.7	0.20	4.54	19	3.7	3.4-4.1	0.20	5.29
M ₂ length	26	6.6	5.5-7.4	0.41	6.28	24	6.1	5.5-7.0	0.35	5.66
width protoloph (-id)	26	4.8	4.2-5.2	0.21	4.33	24	4.4	4.2-4.7	0.15	3.51
M ₃ length	17	6.9	6.0-7.6	0.43	6.23	18	6.5	5.8-7.1	0.39	5.95
width protoloph (-id)	18	4.8	4.5-5.2	0.16	3.35	19	5.0	4.6-5.3	0.18	3.58
M ₄ length	10	6.3	5.5-7.0	0.48	7.68	10	6.0	5.6-6.5	0.37	6.19
width protoloph (-id)	11	4.2	3.8-4.7	0.27	6.52	10	4.6	4.1-4.9	0.26	5.71

between those from the anterior and posterior cuspids; anterior cingula of molars are broad.

Comparison with recent species is difficult because of poor representation of eastern Australian species of *Bettongia* in collections, and some taxonomic uncertainty regarding the material that is held. Wakefield (1967) has reviewed *Bettongia* and on the basis of information presented there, together with the figure of the skull of the holotype of *B. gaimardi* illustrated in Quoy and Gaimard (1842), F6134 compares better morphologically with this species than with others currently known. It is, however, much smaller.

Finlayson (1959) has recorded a 'microdont phase of *B. cuniculis*' in subfossil South Australian collections suggesting that size alone may not be a sufficient basis for separation within the genus.

Subfamily STHENURINAE

Sthenurus oreas De Vis, 1895

Bartholomai (1963) described and figured a partial maxilla, F3814, which was referred to this species. No other specimens referable to *Sthenurus* have been located as yet in the Cement Mills deposits.

Procoptodon cf. *P. rapha* Owen, 1874

(Plate 17, fig. 3)

The single ramus, F4548, compared with *P. rapha* by Bartholomai (1970), shows reduced ornamentation of teeth but is otherwise inseparable from that species. It may represent extreme intraspecific variation, but in the absence of intermediaries, its assignment cannot be made with certainty.

Subfamily MACROPODINAE

Protemnodon anak Owen, 1874

(Plate 17, fig. 10)

Protemnodon anak is represented by two juvenile specimens, F7639 and F7641, in the Cement Mills deposits. These mandibles are morphologically inseparable from the eastern Darling Downs sample (Bartholomai, 1973). Their measurements are included in Table 1.

Protemnodon brehus (Owen, 1874)

(Plate 17, fig. 14)

An isolated left M_4 , F7338, is referred to *P. brehus*. This is morphologically identical to eastern Darling Downs material revised by Bartholomai (1973). Measurements for this specimen are presented in Table 1.

Protemnodon roechus Owen, 1874

(Plate 17, fig. 11)

Two mandibular specimens are referred to *P. roechus*. A partial left mandibular ramus, F7336, is small compared with the bulk of the eastern Darling Downs sample examined by Bartholomai (1973), falling near lower limits for tooth size in that population. Its measurements are provided in Table 1. The posterior cingulum in M_4 in F7336, is well-defined, rare in the eastern Darling Downs sample. The second specimen, an isolated right I_1 , is also small compared with the Darling Downs material.

Thylogale sp.

(Plate 17, fig. 2)

The single specimen referred to *Thylogale* sp., F7353, is a partial adult right ramus with M_1 - M_2 . As seen in Table 1, teeth are small but they compare

well with small individuals of modern *T. thetis* and *T. stigmatica* in the Queensland Museum collections. Links appear slightly less developed in the fossil. Large samples would be required to provide specific identification within this genus.

Macropus giganteus Shaw, 1790

(Plate 17, fig. 6)

M. giganteus is represented by three specimens, F2766, a partial left ramus with DP_3 - M_3 , P_3 excavated, F7878, a partial left ramus with DP_3 - M_2 , P_3 excavated, and F7354, a partial right maxilla with M^2 - M^3 . Measurements for these are provided in Tables 1 and 2. Compared with measurements for recent *M. giganteus* in Bartholomai (1971a), the teeth in F2766 are relatively more elongate than usual, but this difference is not considered significant.

Macropus titan Owen, 1838

(Plate 17, fig. 13)

The extinct *M. titan* is known from only one specimen, F7633, an isolated, unerupted left M^3 . Its measurements are presented in Table 2. In size and morphology, this specimen is within the range indicated for eastern Darling Downs specimens considered by Bartholomai (1975).

Macropus cf. ***M. agilis siva*** (De Vis, 1895)

(Plate 17, fig. 5)

The specimens referred to *Macropus* cf. *M. agilis siva* agree in size, but differ slightly in morphology from the large eastern Darling Downs sample considered by Bartholomai (1975). F7640, a partial left maxilla with P^3 - M^3 , differs in lacking any trace of an accessory link on the trigonid in anterior molars. This feature is not present in all specimens

TABLE 7: SUMMARY OF MEASUREMENTS FOR *Macropus dorsalis*, CEMENT MILLS SAMPLE

Character	Maxillae					Mandible				
	n	X	O.R.	s	V	n	X	O.R.	s	V
P_2^1 length	1	5.0	—	—	—	1	5.0	—	—	—
width posteriorly	—	—	—	—	—	1	2.6	—	—	—
DP_3^1 length	2	5.7	5.4-6.0	0.42	7.44	3	5.93	5.8-6.1	0.15	2.57
width protoloph (-id)	1	4.0	—	—	—	3	3.47	3.2-4.0	0.46	13.32
P_3^1 length	2	6.45	6.3-6.6	0.21	3.29	1	5.9	—	—	—
width posteriorly	1	3.0	—	—	—	—	—	—	—	—
M_1^1 length	7	6.37	6.0-7.3	0.43	6.82	7	6.63	6.2-7.4	0.38	5.76
width protoloph (-id)	5	4.68	4.3-5.3	0.38	8.05	7	4.07	4.0-4.2	0.08	1.86
M_2^1 length	10	7.66	6.8-8.9	0.72	9.40	10	7.25	5.9-8.4	0.80	11.02
width protoloph (-id)	6	5.90	5.3-6.4	0.55	9.35	13	4.68	4.1-5.6	0.36	7.79
M_3^1 length	8	8.55	7.7-9.7	0.67	7.78	16	8.31	7.8-8.8	0.33	3.97
width protoloph (-id)	8	6.18	5.4-7.1	0.63	10.20	17	5.36	4.9-5.7	0.21	3.90
M_4^1 length	4	8.93	8.2-9.2	0.49	5.44	10	8.65	8.3-9.2	0.27	3.09
width protoloph (-id)	4	6.55	6.2-6.7	0.24	3.63	12	5.62	5.3-5.8	0.13	2.38

in the Darling Downs sample. Measurements for the Cement Mills material are provided in Tables 1 and 2. Definite reference of the material to *M. agilis siva* would be premature.

***Macropus dorsalis* (Gray, 1837)**
(Plate 17, fig. 7)

A reasonably large sample of *M. dorsalis* comprises one partial skull, 13 maxillae, 30 mandibular rami and numerous isolated incisors. The sample is identical with modern material in the collections of the Queensland Museum. As with other larger macropodines, most of the sample has been drawn from juvenile individuals. Summaries of maxillary and mandibular measurements are provided in Table 7.

***Macropus parryi* (Bennett, 1835)**
(Plate 17, fig. 12)

The sample referred to *M. parryi* represents the largest number of individuals in the deposits. It comprises one partial skull, four premaxillae, 24 maxillae, 69 mandibular rami, 10 isolated molars and numerous isolated incisors. Many of the specimens are juvenile. No differences are apparent between this sample and recent *M. parryi* in the Queensland Museum collections. A summary of maxillary and mandibular measurements is provided in Table 8.

EUTHERIA

RODENTIA

Gen. and sp. indet.
(Plate 17, fig. 9)

Rodents are relatively poorly represented in the Cement Mills deposits. Only four specimens have

been recovered, these comprising F7634, a partial left maxilla, F7635, an isolated upper incisor, F7636, a fragmentary partial right ramus and F7637, a partial right mandibular ramus. The material is obviously not hydromyine.

DISCUSSION

The fossil fauna from the cave and fissure-fill deposits at Cement Mills, Gore, southeastern Queensland is a remarkably diverse assemblage of vertebrates. While several taxa are sufficiently well represented to permit statistical evaluation of the population from which they were drawn, the majority reflect small sample numbers.

Within statistically assessed populations it is apparent that somewhat anomalous values for the Coefficient of Variation are sometimes present. The fossil sample of *Perameles nasuta* frequently exhibits lower values for V in the characters examined than does the available living sample. In absolute terms, this living sample compares well with the larger sample of *P. nasuta* examined by Freedman and Joffe (1967), but has some values for V which are higher. It is believed that the anomaly, which is independent of the fossil sample, reflects peculiarities of the modern sample available in the Queensland Museum. High values for V are evident in posterior molars within both the living and fossil samples of the potoroine *Aepyprymnus rufescens*, especially where such values are compared with those for selected macropodines (Bartholomai, 1971a). The fossil sample for *Macropus dorsalis* exhibits a number of abnormal values for V, but in this case, small sample size is most likely responsible. Values more comparable with those

TABLE 8: SUMMARY OF MEASUREMENTS FOR *Macropus parryi*, CEMENT MILLS SAMPLE

Character	Maxillae					Mandible				
	n	X	O.R.	s	V	n	X	O.R.	s	V
P ₂ length	2	5.7	5.1-6.3	0.85	14.89	1	4.5	—	—	—
width posteriorly	2	3.2	2.8-3.6	0.57	17.68	1	2.3	—	—	—
DP ₃ length	1	7.2	—	—	—	9	6.26	5.9-6.7	0.28	4.53
width protoloph (-id)	—	—	—	—	—	8	3.31	2.9-3.9	0.30	9.05
P ₃ length	3	6.4	5.7-7.3	0.82	12.79	15	4.20	3.7-4.8	0.34	8.00
width posteriorly	3	3.17	2.7-3.9	0.64	20.30	6	2.22	2.1-2.4	0.12	5.27
M ₁ length	14	7.29	6.6-8.2	0.38	5.23	36	6.73	5.8-7.6	0.47	7.03
width protoloph (-id)	12	5.76	5.5-6.0	0.18	3.18	35	4.23	3.8-5.00	0.29	6.92
M ₂ length	18	8.51	8.1-9.1	0.31	3.67	36	7.82	6.8-8.8	0.47	6.02
width protoloph (-id)	18	6.45	5.9-7.0	0.27	4.23	36	5.00	4.6-5.7	0.27	5.34
M ₃ length	12	9.50	8.9-10.3	0.40	4.16	34	8.70	8.0-9.2	0.30	3.40
width protoloph (-id)	11	7.13	6.6-8.0	0.41	5.82	36	5.74	5.1-6.2	0.23	4.07
M ₄ length	6	9.30	8.9-9.7	0.30	3.26	13	9.15	8.8-9.7	0.24	2.62
width protoloph (-id)	8	6.88	6.6-7.2	0.21	3.09	19	5.84	5.4-6.2	0.18	3.09

provided for other macropodines in Bartholomai (1971a) are evident in the large sample of *M. parryi* examined.

From the relatively large numbers of marsupial carnivores represented, comprising *Dasyurus* aff. *D. viverrinus*, *Sarcophilus lanarius*, *Thylacinus cynocephalus* and *Thylacoleo carnifex*, it is apparent that the caves and fissures acted as lairs during the past. This is supported by the fragmentary and juvenile nature of much of the material, although bones exhibiting tooth marks have not been recorded. Small to medium-sized herbivores are especially well represented. Undoubtedly, however, some bone was contributed by wash and fill processes.

A relatively high proportion of the fauna is of recent species or of forms closely related to living species. Compared with the recorded fauna from the Pleistocene fluviatile deposits of the eastern Darling Downs, this difference is particularly apparent. Fossil species predominate in the Darling Downs deposits. Sufficient extinct species are present at Cement Mills to indicate that most of the sediments were accumulated during the Pleistocene. However, some of the fauna was probably deposited late in the Pleistocene or even in Recent times. There is an absence of evidence for stratification within the deposits, but the presence of both *Macropus titan* and *M. giganteus* suggests that different times of deposition are most likely involved. Bartholomai (1975) has suggested the possibility of close phylogenetic relationships between *M. titan* and *M. giganteus*.

The presence of species such as *Perameles nasuta*, *Potorous* aff. *P. tridactylus* and *Thylogale* sp., usually found in rain forests, in an assemblage which could otherwise be interpreted as representing an open sclerophyll situation further suggests that deposition was over a time sufficient to permit fluctuations of climate to influence the habitats in the close vicinity.

One taxon, *Palorchestes* cf. *P. parvus* is problematical in this interpretation of the age of deposition. Woods (1958) has shown that *P. parvus* is most likely known only from the Chinchilla Sand, now regarded as being of Late Pliocene age (Bartholomai, 1973). However, the Cement Mills record is an isolated specimen and as such could ultimately prove distinct, or could involve an extension of range for *P. parvus*. It is considered less likely that older deposits are represented at Cement Mills.

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PLATE 16

- FIG. 1: *Tiliqua scincoides* (Shaw, 1790). Lateral view of left mandibular ramus, F7709, $\times 2$.
- FIG. 2: *Phascolomis* c.f. *P. magnus* Owen, 1872. Lateral view of isolated molar tooth, F7351, $\times 1$.
- FIG. 3: *Sarcophilus lanarius* (Owen, 1838). Lateral view of left mandibular ramus, F3705, $\times 1$.
- FIG. 4: *Dasyurus* aff. *D. viverrinus* (Shaw, 1800). Lateral view of left mandibular ramus, F3703, $\times 1$.
- FIG. 5: *Thylacoleo carnifex* Owen, 1859. Occlusal view of right mandibular ramus, F5708, $\times 0.5$.
- FIG. 6: *Perameles nasuta* Geoffroy, 1804. Occlusal view of partial skull, F7854, $\times 1$.
- FIG. 7: *Thylacinus cynocephalus* (Harris, 1808). Lateral view of right mandibular ramus, F3737, $\times 1$.
- FIG. 8: *Palorchestes* cf. *P. parvus* De Vis, 1895. Occlusal view of right maxilla, F7340, $\times 1$.
- FIG. 9: *Vombatus ursinus* (Shaw, 1800). Occlusal view of left mandibular ramus, F2774, $\times 1$.
- FIG. 10: *Palorchestes azael* Owen, 1874. Occlusal view of isolated premolar, F3836, $\times 1$.
- FIG. 11: *Aepyprymus rufescens* (Gray, 1837). Occlusal view of partial skull, F4768, $\times 1$.
- FIG. 12: *Isoodon* sp. Occlusal view of right maxilla, F2773, $\times 2$.
- FIG. 13: *Phascolonius gigas* (Owen, 1859). Lateral view of right mandibular ramus, F2772, $\times 0.5$.

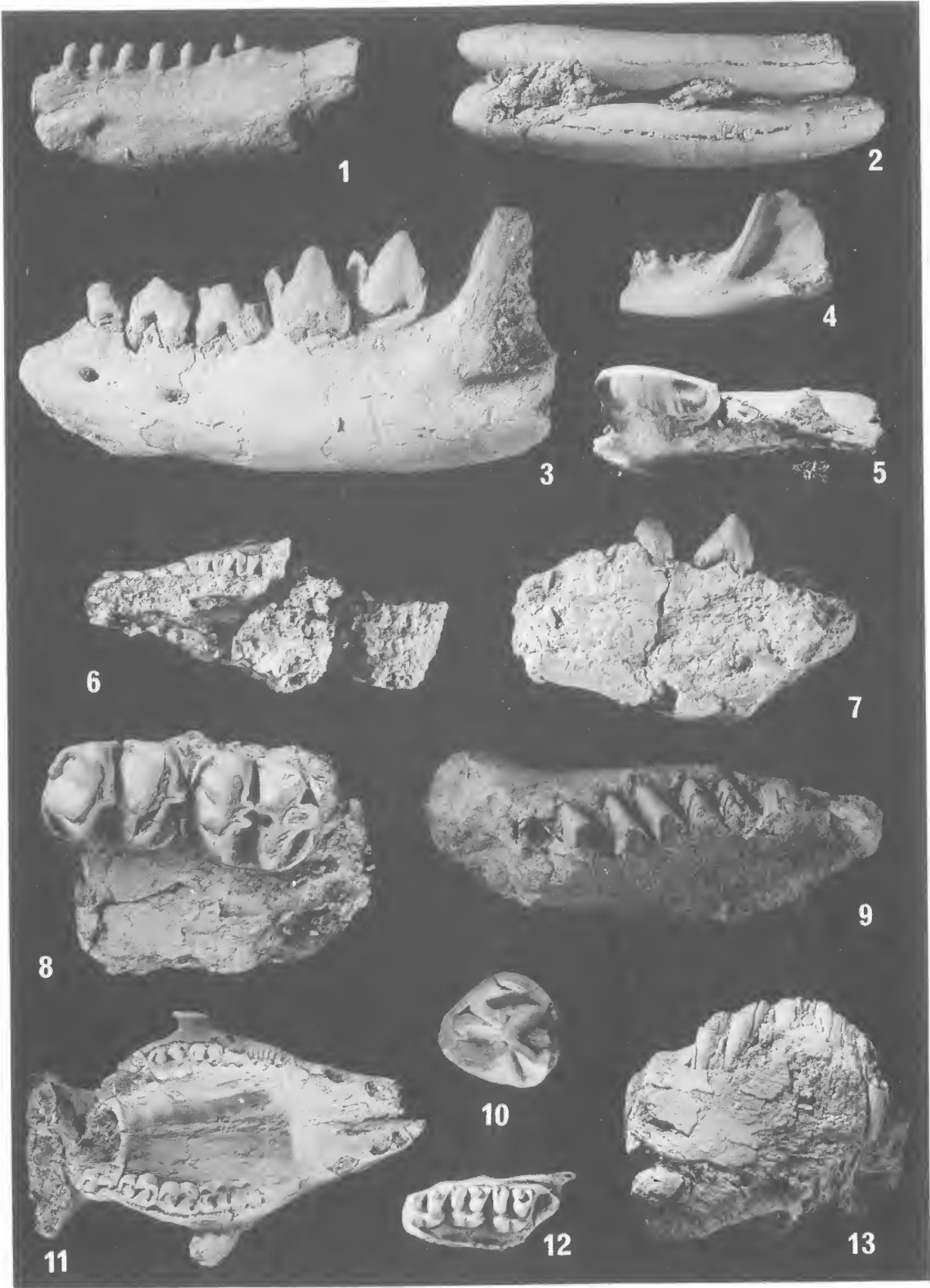
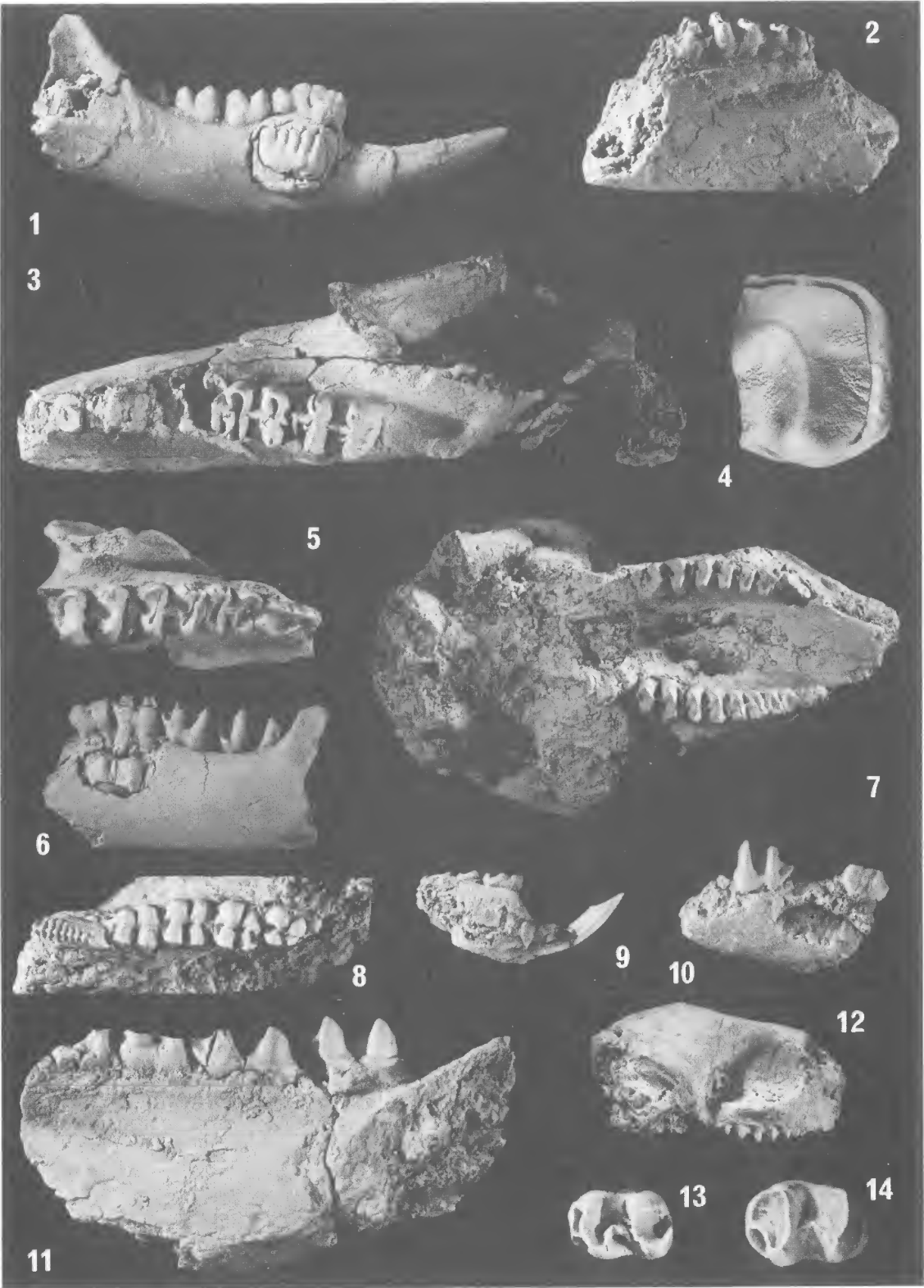


PLATE 17

- FIG. 1: *Potorous* aff. *P. tridactylus* (Kerr, (1792). Lateral view of right mandibular ramus, F6092, $\times 2$.
- FIG. 2: *Thylogale* sp. Lateral view of right mandibular ramus, F7353, $\times 2$.
- FIG. 3: *Procoptodon* cf. *P. rapha* Owen, 1874. Occlusal view of right mandibular ramus, F4548, $\times 0.5$.
- FIG. 4: *Nototherium inerme* Owen, 1845. Occlusal view of partial molar tooth, F7339, $\times 1$.
- FIG. 5: *Macropus* cf. *M. agilis siva* (De Vis, 1895). Occlusal view of right maxilla, F7640, $\times 1$.
- FIG. 6: *Macropus giganteus* Shaw, 1790. Lateral view of left mandibular ramus, F7878, $\times 1$.
- FIG. 7: *Macropus dorsalis* (Gray, 1837). Occlusal view of partial skull, F7676, $\times 1$.
- FIG. 8: *Bettongia* sp. Occlusal view of right mandibular ramus, F6134, $\times 2$.
- FIG. 9: Rodentia. Lateral view of right mandibular ramus, F7637, $\times 2$.
- FIG. 10: *Protemnodon anak* Owen, 1874. Lateral view of right mandibular ramus, F7639, $\times 1$.
- FIG. 11: *Protemnodon roechus* Owen, 1874. Lateral view of left mandibular ramus, F7336, $\times 1$.
- FIG. 12: *Macropus parryi* (Bennett, 1835). Lateral view of partial skull, F7675, $\times 0.5$.
- FIG. 13: *Macropus titan* Owen, 1838. Occlusal view of isolated molar tooth, F7633, $\times 1$.
- FIG. 14: *Protemnodon brehus* (Owen, 1874). Occlusal view of isolated molar tooth, F7338, $\times 1$.





TERRESTRIAL MOLLUSCA OF QUEENSLAND: THE FAMILY VERONICELLIDAE

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In Queensland there are two species of slugs of the family Veronicellidae, *Laevicaulis alte* and *Vaginulus plebeius*. A general description of their anatomy is given together with the diagnostic features by which they may be identified. The known Queensland distributions are listed. They are economically important as pests of cultivation and as vectors of vertebrate nematode infections.

The only illustrated account which attempts to deal with the terrestrial mollusc fauna of Australia as a whole is the monograph of Cox (1868). Many problems are therefore experienced in attempting identifications. The check list of Iredale (1937-38) provides a guide to the literature but is uncritical at the species level. Iredale's higher taxa have caused considerable difficulties because of a lack of comparative studies with taxa outside Australia. Zilch (1960) appends a list of over 260 of Iredale's generic names which he was unable to include in the text. Solem (1959) has presented valuable conclusions as to the nature of some of Iredale's genera and families. A number of other papers deal with particular groups but much more research is needed before an adequate monograph can be produced. The present paper is a contribution towards this end.

METHODS

This study is based on material held in the Australian Museum (C series), National Museum of Victoria (F series) and the Queensland Museum (MO series) including recent collections by the author. The reference numbers are the Museum registration numbers applied to each specimen lot. Material is preserved in 70% alcohol or 4% formalin. Dissections were performed with the specimen under water, using fine watchmakers forceps, and drawn with the help of the camera lucida. Jaws and radulae were extracted from the buccal mass in a solution of sodium hydroxide (10%). Names quoted in synonymy refer to Queensland material. Distribution records are grouped according to the half degree 'squares' of latitude

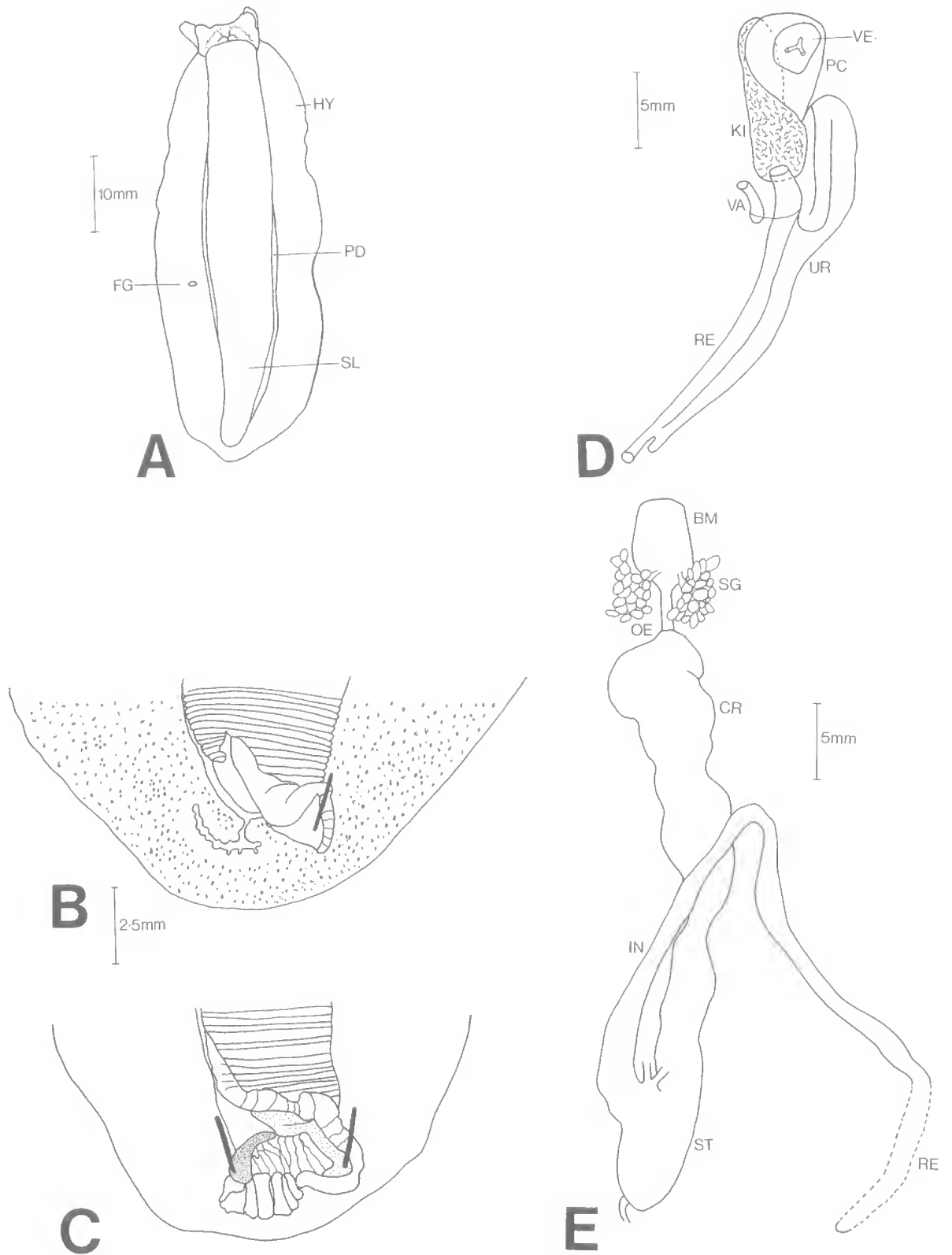
and longitude of the Australian Geodetic Datum (Goodrick 1974).

SYSTEMATIC ACCOUNT

Family VERONICELLIDAE

A key to the families of Australian terrestrial slugs is given by Altena and Smith (1975). The species of Veronicellidae are not natives of Australia but were accidentally introduced by man. Members of the family are found throughout the wet tropical regions of the world and some extend to sub-tropical areas. The fullest account of the biology and anatomy of the Veronicellidae is given by Hoffmann (1925). The nomenclature used is not correct, as Baker (1925) pointed out, and I am following the generic assignments used by Forcart (1969). Simroth (1889) described two new species on the basis of Queensland material without making any anatomical studies. Grimpe and Hoffman (1925) examined Simroth's types preserved in the Berlin Museum and placed his names into synonymy.

EXTERNAL FEATURES: The animals are pulmonate slugs without a shell (internal or external) and without a mantle cavity. There is a convex dorsal integument (notum) which extends down over the head. The notum is separated from its ventral extension (hypnotum) by a sharp keel (perinotum). The ventral surface has a central foot sole separated by a pedal groove from the hypnota (Fig. 1A). A pedal gland lies free in the body cavity and opens below the mouth. The head bears two pairs of tentacles, the upper pair (ommatophores)



have eyes on contractile stalks, while the lower pair are bifid with a sensory end bulb (Fig. 2C). The anus opens behind the foot, slightly to the right of the mid-line. The female genital opening is midway on the right hypnotum (Fig. 1A) and the male genital opening is on the right side of the mouth in the pedal groove (Fig. 2C).

PALLIAL COMPLEX: The pallial complex (Fig. 1D) is situated within the right body wall. The kidney lies along the right side of the pericardium and partly beneath it at the posterior end, extending to where the hindgut enters the body wall. The ureter is S-shaped and contains spongy highly vascularised tissue. The last arm is enlarged and opens into the rectum near the anus.

DIGESTIVE SYSTEM: The buccal mass contains the jaw which is formed of narrow vertical plates and the radula which is composed of unicuspid teeth. In each tooth row of the radula the central tooth is narrow and there are many broader lateral teeth. A pair of salivary glands drain into the buccal cavity (Fig. 1E). A narrow oesophagus leads from the buccal mass to the large crop. From the stomach there are a number of openings to the lobes of the digestive gland. This voluminous gland covers most of the dorsal aspect of the viscerae. The intestine loops forward to enter the body wall on the right side and the rectum receives the ureter before opening at the anus.

CENTRAL NERVOUS SYSTEM: The paired cerebral ganglia lie above the oesophagus. From these ganglia connectives pass to the paired buccal ganglia on the surface of the buccal mass. Ventrally there are two pedal ganglia and a visceral chain formed by the fusion of five component ganglia into one mass. The point of divergence of the pedal nerves on the floor of the body cavity is variable within the family.

RETRACTOR MUSCLES: Left and right cephalic, buccal and genital retractors all arise separately on the body wall. This is the situation to be expected in the absence of a shell of any kind.

REPRODUCTIVE SYSTEM: The reproductive system (Figs. 2–3) is hermaphrodite but the male portion appears to develop before the female. The hermaphrodite duct leads from the ovotestis to the carrefour or junction with the male and female

tracts. Before the junction there may be a small diverticulum, the fertilisation pocket. The female tract consists of a long oviduct which receives the albumen gland near the carrefour and leads to the muscular vagina opening on the right hypnotum. The bursa copulatrix is connected to the vagina by a pedicle and to the male system by the canalis junctor. There may be an accessory bursa attached to the vagina near its opening. The male tract commences with the vas deferens which receives the prostrate gland near the carrefour, gives off the canalis junctor, and enters the body wall associated with the vagina. From here it passes forward to emerge near the penial complex situated to the right of the buccal mass. The penial complex comprises the intromittent penial verge and the penial stimulator with its gland consisting of a bunch of tubules. The verge and stimulator are enclosed in a thin sheath and are supplied with retractor muscles.

Genus *Laevicaulis* Simroth (1913)

TYPE SPECIES: *Vaginula comorensis* Fischer (1883) by subsequent designation of Pilsbry (1919).

The retracted foot does not extend over the anus. The anal opening is a crescentic slit. The pedal gland is kinked. The pedal nerves diverge from their point of origin. The anterior curve of the intestine lies in front of the digestive gland. The salivary glands are compact. The vagina and hindgut are close together at their point of entry to the body wall. The verge is cylindrical with an annular swelling near the base, and the opening of the vas deferens is terminal. The penial stimulator is short and conical.

Laevicaulis alte (Férussac)

Vaginulus alte Férussac, 1821, p. 14.

Vaginula leydigi Simroth, 1889, pp. 552–6. Odhner, 1917, p. 89.

Meisenheimeria alte; Grimpe and Hoffmann, 1925, pp. 26–31.

Meisenheimeria leydigi; Iredale, 1938, p. 122.

TYPE LOCALITY: Pondicherry, India.

DIAGNOSTIC FEATURES: Distinguished from *V. plebeius* externally by the anal aperture in the form of a crescentic slit and internally by the long cylindrical penis with sub-basal collar and terminal opening of the vas deferens.

FIG. 1: A–B *Laevicaulis alte* (Férussac). A Ventral aspect and B anal orifice (MO5798, Kallangur).

C–E *Vaginulus plebeius* Fischer. C Anal orifice (MO5801, Coorparoo); D pallial complex (MO4127, Indooroopilly); E digestive system (MO5802, New Farm).

BM buccal mass, CR crop, FG female gonopore, HY hypnotum, IN intestine, KI kidney, OE oesophagus, PC pericardium, PD pedal groove, RE rectum, SG salivary gland, SL foot sole, ST stomach, UR ureter, VA vagina, VE ventricle.

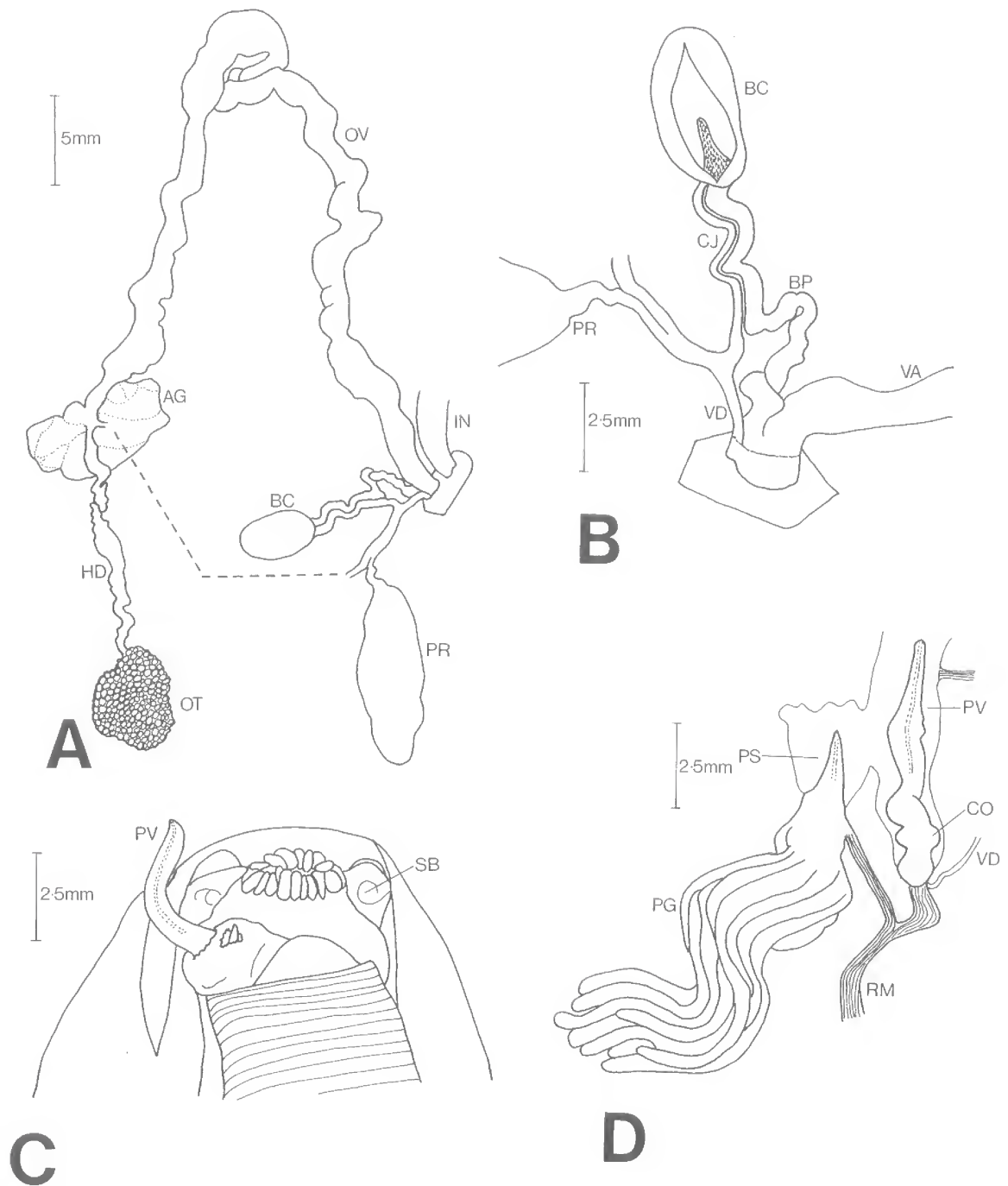


FIG. 2: *Laevicaulis alte* (Férussac). A–B Genitalia (MO4462, Point Lookout); C extruded penial verge and stimulator (MO1615, Brisbane); D penial complex (MO4283, Upper Mt. Gravatt).

AG albumen gland, BC bursa copulatrix, BP bursa pedicle, CJ canalis junctor, CO collar, HD hermaphrodite duct, IN intestine, OT ovotestis, OV oviduct, PG penial gland, PR prostate, PS penial stimulator, PV penial verge, RM retractor muscle, SB sensory bulb, VA vagina, VD vas deferens.

EXTERNAL FEATURES: Length (alcohol material) 62, 50 mm (MO4126), 52 mm (MO4283). The notum is pigmented with dark brown or gray with a lighter yellowish band down the midline. The hypnotum is light in colour. A live animal is illustrated in Plate 12A. The anal aperture is a crescentic slit with a conspicuous pale border (Fig. 1B). The kinked pedal gland is figured by Oberzeller (1970, Fig. 2). The female gonopore is close to the pedal groove. The position of the partially extruded penial verge and stimulator is shown in Fig. 2C from a preserved specimen.

DIGESTIVE SYSTEM: The radula, jaw and digestive tract are figured by Oberzeller (1970, Fig. 3–5). The salivary glands are a whitish compact mass.

REPRODUCTIVE SYSTEM: The hermaphrodite duct has a small fertilisation pocket. The prostate is large in the figured specimen (Fig. 2A). The bursa copulatrix has a long pedicle which protrudes into the bursa as a papillate extension. The verge is long and cylindrical with a sub-basal collar and terminal opening of the vas deferens. The penial stimulator is short and conical with a single insertion of the retractor muscle (Fig. 2D). The penial gland has about 18 tubules.

QUEENSLAND DISTRIBUTION: 9°30'S. 144°00'E. Murray Is. (C104230); 15°00'S. 145°00'E. Cooktown (C5731, C104236); 16°30'S. 145°30'E. Yarrabah (Odhner, 1917); 17°00'S. 145°00'E. Atherton (Odhner, 1917); 18°00'S. 146°00'E. Hinchinbrook Is. (C54496); 23°00'S. 150°00'E. Rockhampton (C104231); 23°00'S. 150°30'E. Yeppoon (C104244, F30010); 23°00'S. 151°30'E. Heron Is. (F30009), Nor' West Is. (C104233–4, F13512); 27°00'S. 152°30'E. Kallangur (MO5798); 27°00'S. 153°00'E. Brisbane (C96, MO1615–17, 1762), Fortitude Valley (MO1791), St. Lucia (MO4126); 27°00'S. 153°30'E. Point Lookout (F30013, MO4462); 27°30'S. 153°00'E. Ormiston (MO5799), Salisbury (MO3032), Upper Mt. Gravatt (MO4283); 28°00'S. 152°00'E. Burleigh Heads (F30011).

RANGE: The species is thought to have originated in southern Asia (possibly India) and to have been widely spread in the Indian Ocean and Pacific regions by commerce. The recorded Queensland distribution is doubtless incomplete and the species is to be expected in suburban and cultivated areas throughout the moist eastern seaboard of the State.

ECOLOGY: The Veronicellidae are nocturnal herbivores or omnivores eating both green plants and decaying organic material. They may cause damage in gardens and horticultural nurseries and

may be difficult to control even with the use of slug bait (metaldehyde). Little seems to be known about the life history and general biology of *L. alte*.

Genus *Vaginulus* Férussac (1821)

TYPE SPECIES: *Vaginulus taunaisii* Férussac (1821) by subsequent designation of Stoliczka (1873).

The retracted foot extends over the anus. The anal opening is protected by a flap on the right. The pedal nerves do not immediately diverge. All intestinal loops are embedded in the digestive gland. The pedicle of the bursa copulatrix is short or absent. The penis is somewhat asymmetrical with the opening of the vas deferens subterminal.

Vaginulus plebeius Fischer

Vaginulus plebeius Fischer, 1868, p. 146.

Vaginula Hedleyi Simroth, 1889, pp. 552–556.

Vaginula hedleyi; Odhner, 1917, p. 89.

Sarasinula plebeja; Grimpe and Hoffmann, 1925, pp. 25–26.

Sarasinula hedleyi; Iredale, 1938, p. 123.

TYPE LOCALITY: New Caledonia.

DIAGNOSTIC FEATURES: Distinguished from *L. alte* externally by the dextral flap covering the anal aperture and internally by the swollen asymmetrical penial verge with subterminal opening of the vas deferens.

EXTERNAL FEATURES: Length (alcohol material) 58, 54 mm (MO5801), 47 mm (MO4127). The notum is pigmented light brown with black points particularly on each side of the midline. The hypnotum is light in colour. A live animal is illustrated in Plate 12B. The anal aperture is covered by a flap on the right side which when lifted reveals a deep wide pit (Fig. 1C). The female gonopore is about half way between the pedal groove and the perinotum. The straight pedal gland is figured by Hoffmann (1925, Fig. 5A).

DIGESTIVE SYSTEM: The radula is figured by Hoffmann (1925, Fig. 8q). The salivary glands are yellowish and in the form of bunches of grapes (Fig. 1E).

REPRODUCTIVE SYSTEM: The individual figured (Fig. 3A) appeared sub-adult. There is no fertilisation pocket in the hermaphrodite duct. The prostate is small. The bursa copulatrix has a short pedicle continued into the bursa as an extension without papillae. The verge is asymmetrical with a subterminal opening of the vas deferens. Baker (1931, plate 8, fig. 2) showed how the verge does not

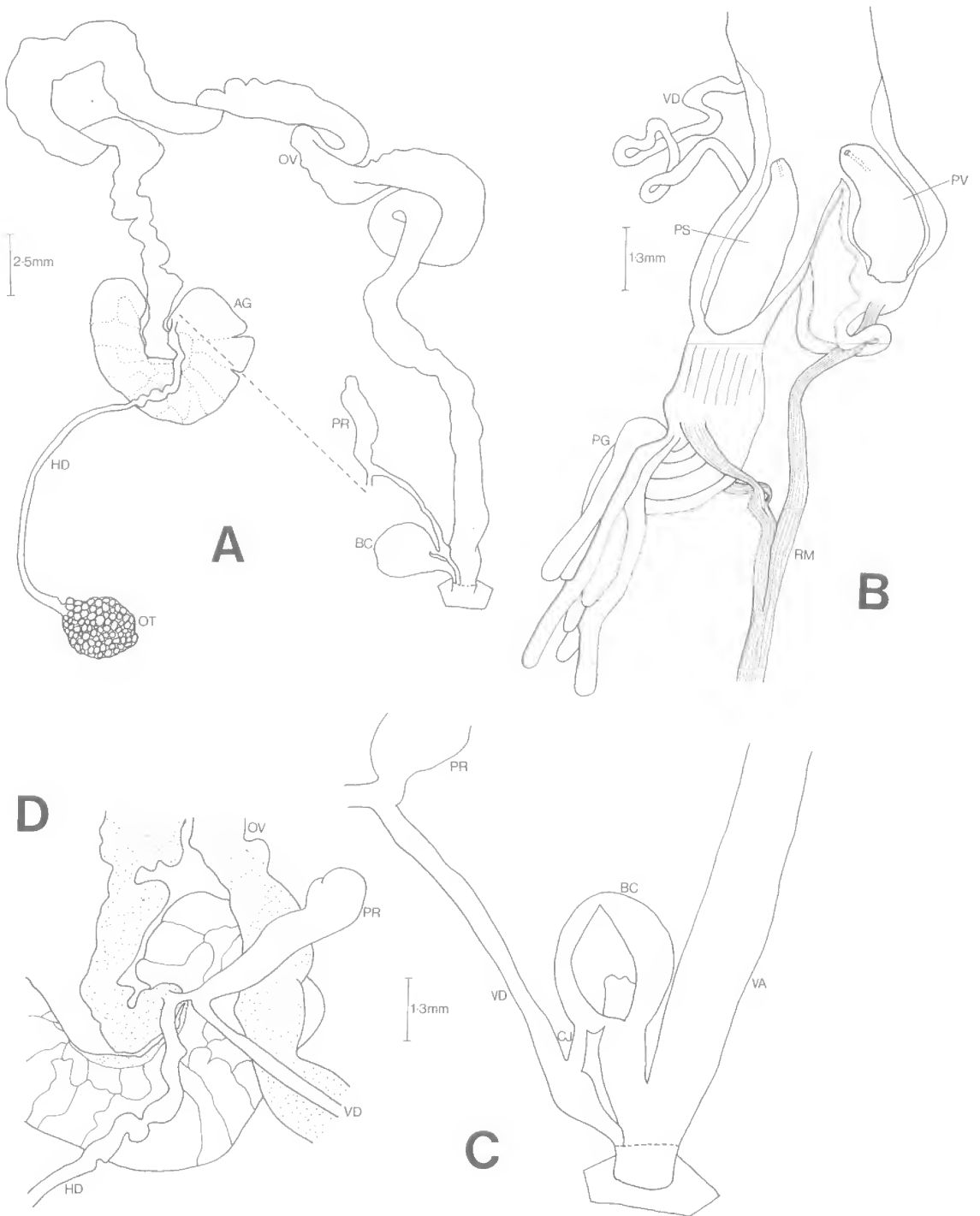


FIG. 3: *Vaginulus plebeius* Fischer. A Genitalia, B penial complex, C region of bursa copulatrix (MO5802, New Farm); D details of carrefour (MO5801, Coorparoo).

AG albumen gland, BC bursa copulatrix, CJ canal junction, HD hermaphrodite duct, OT ovotestis, PG penial gland, PR prostate, PS penial stimulator, PV penial verge, RM retractor muscle, VA vagina, VD vas deferens.

have a terminal papilla but has a broad weakly emarginate flap which appears as a papilla in side view. The penial stimulator is long and broad with a double insertion of the retractor muscle (Fig. 3B). The penial gland has about 6–8 tubules.

QUEENSLAND DISTRIBUTION: 13°30'S. 143°00'E. Coen (F30014); 15°00'S. 145°00'E. Cooktown (C104529); 16°30'S. 145°30'E. Cairns (C104243); 17°00'S. 145°00'E. Atherton, Herberton (Odhner, 1917), Tinaroo Dam (F30012); 19°00'S. 146°30'E. Townsville (C104240-1); 20°00'S. 148°30'E. Proserpine R. (C104187); 21°00'S. 149°00'E. Sarina (C104237, juv. only); 23°00'S. 150°00'E. Rockhampton (C104235); 27°00'S. 153°00'E. Brisbane (C95, 104239); Kangaroo Point (MO5805), New Farm (MO5802), Redcliffe (MO5803); 27°30'S. 152°30'E. Chelmer (MO1964), Indooroopilly (MO4127, 5804); 27°30'S. 153°00'E. Coorparoo (MO5801), Ormiston (MO3450); 28°00'S. 148°30'E. St. George (C104238, juv. only).

RANGE: The species is thought to have originated in the tropical American region. It has been widely spread by commerce in the Indian Ocean and Pacific regions. It is to be expected in regions of cultivation along the east Queensland coast.

ECOLOGY: As in the case of *L. alte* this species may become a pest in gardens. *V. plebeius* acts as a secondary host for certain nematode infections of vertebrates and has even been implicated in human disease (Modera and Céspedes, 1973).

ACKNOWLEDGMENTS

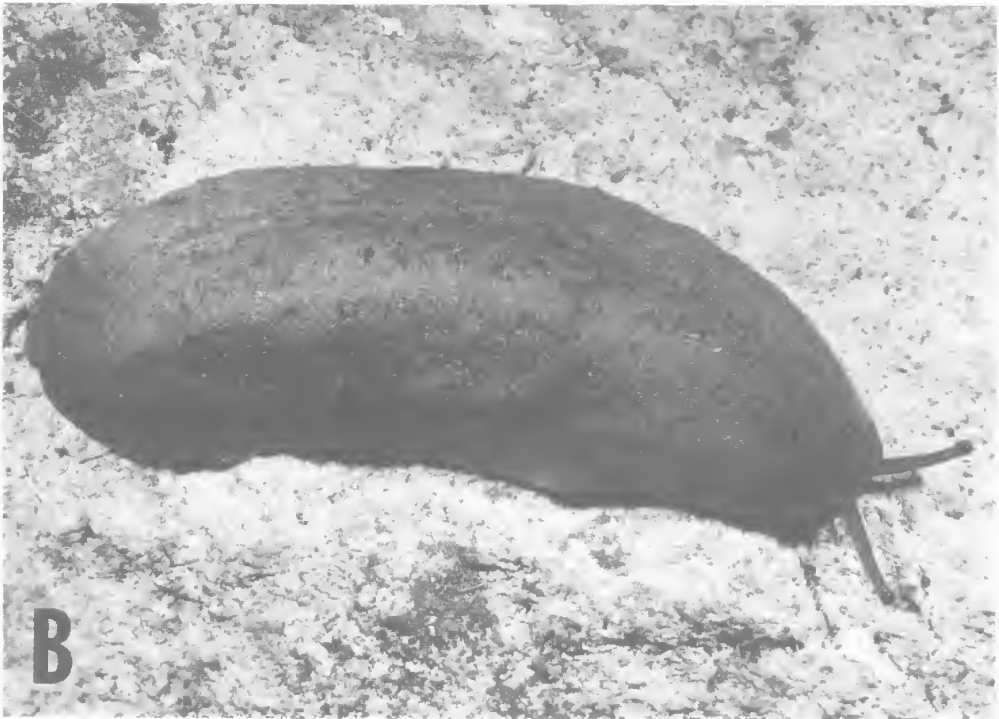
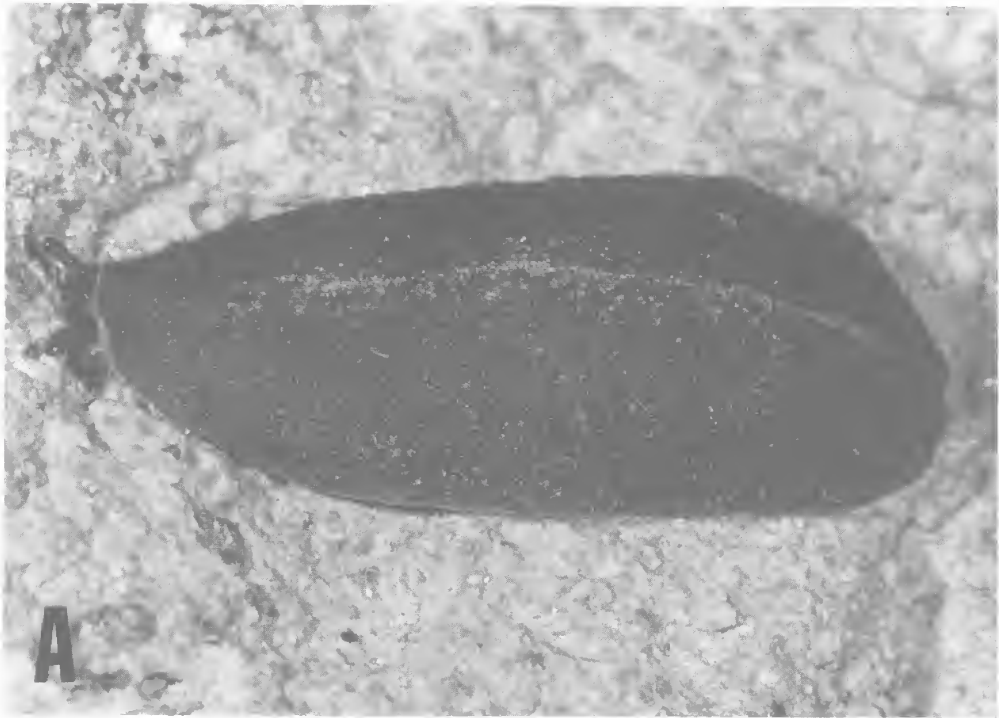
I am grateful to Dr A. Waddell for providing material and for pointing out the medical importance of these slugs to me. I thank Mr. P. Colman (Australian Museum) and Dr B. J. Smith (National Museum of Victoria) for sending material from the collections.

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PLATE 18

- A: *Laevicaulis alte* (Férussac), dorsal view of a live individual from Kallangur (MO5798) length 53 mm.
B: *Vaginulus plebeius* Fischer, dorsal view of a live individual from Coorparoo (MO5801) length 56 mm.





NEOPURCELLIA CAPRICORNIA, A NEW OPILIONID (OPILIONES:
CYPHOPHTHALMI: SIRONIDAE: SIRONINAE) FROM QUEENSLAND
AUSTRALIA

VALERIE TODD DAVIES
Queensland Museum

ABSTRACT

Neopurcellia capricornia sp. nov. is the second cyphophthalmid to be described from Australia.

The cyphophthalmids are small mite-like Opiliones which are characterised by their granulate integument, the possession of a pair of odoriferous glands opening dorsally on mounds on the cephalothorax and the absence of a genital operculum. They are usually blind. The sub-order Cyphophthalmi consists of one family, Sironidae which is divided into two sub-families Stylocellinae and Sironinae. The Australian and New Zealand genera belong to the sub-family Sironinae in which the anterior coxae are movable. When Forster (1955) described the first cyphophthalmid from Australia he placed it in the genus *Rakaia* Hirst which was already represented in New Zealand by 20 species. So it is not surprising that this species should belong to the other New Zealand genus, *Neopurcellia* which has three N.Z. species. *Neopurcellia* is characterised by the bipartite tarsus IV of the male.

Neopurcellia capricornia sp. nov.
Figs. 1–13

MATERIAL EXAMINED

HOLOTYPE: Queensland Museum QM W5765, ♂; litter, rainforest, Finch Hatton, mid-eastern Queensland; collected V. Davies and R. Kohout, 10.iv.75.

PARATYPE: QM W5766, ♀; same data as holotype.

DESCRIPTION OF MALE

COLOUR: Red brown body with light yellow brown appendages and light area round the odoriferous gland openings. An indistinct dark line mid-dorsally.

BODY: Body length 2.00mm, cephalothorax width 1.16mm, abdomen width 1.16mm. Body surface granulate (Fig. 1) with sparse hairs increasing in length towards the posterior end. Odoriferous glands open on mounds about twice their

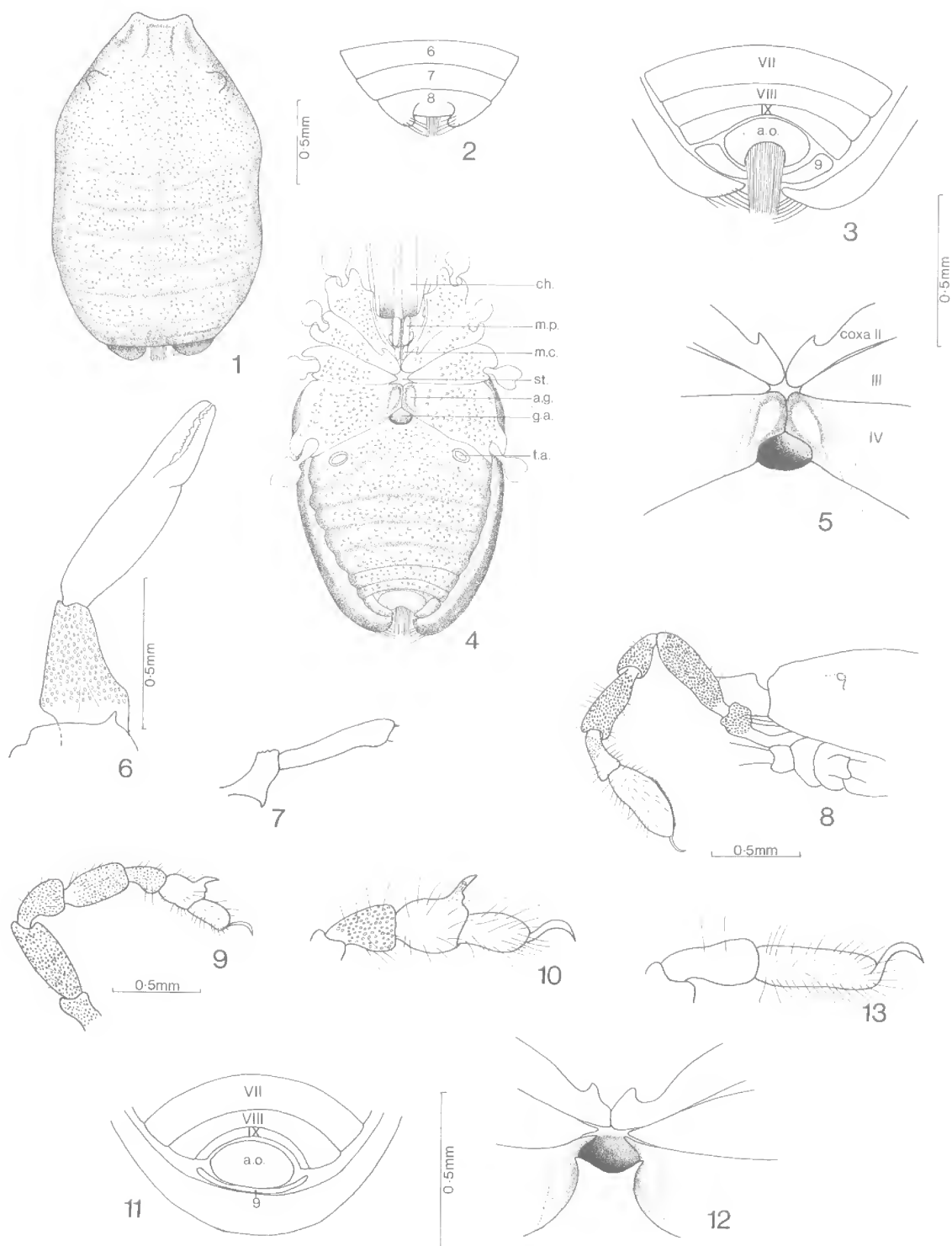
basal diameter from the lateral margin of the cephalothorax (Fig. 8) and about six diameters apart. Tergites clearly defined by transverse areas which are less granulate; tergites 7 and 8 with a shallow median groove; tergite 8 with rounded posterior projections (Fig. 2); tergite 9 divided and tucked under ventrally to form posterior part of corona analis (Fig. 3). A thick scopula of shiny 'hair' posterior to the anal operculum. Lateral margins of the abdomen with a rim formed by the folding over of the dorsal chitin, this rim including rounded projections of tergite 8.

Between coxae I on the ventral surface (Fig. 4) the soft manducatory parts of the coxae of the pedipalps and of coxae I are seen. The arculi genitales, representing the first abdominal sternite are delineated by a groove from coxae IV and border the genital aperture laterally and anteriorly. The aperture is wider than long, 1.75:1, and is well separated from coxae III by the ridges of the arculi genitales (Fig. 5). The second abdominal sternite is believed to be fused with the third and bears the genital aperture and the tracheal openings. Sternites IV–IX are clearly delineated.

CHELICERA: Basal segment (0.60mm) evenly granulate on all surfaces except the ventral which is smooth; lateral edges extended ventrally; dorsal transverse ridge present. Second segment (0.84mm) smooth. Two types of teeth on the inner surface of the chela (Fig. 6).

PEDIPALP: Trochanter with ventral process (Fig. 7). Trochanter and femur finely granulate surface, other segments smooth. Tibia slightly shorter than tarsus, 0.93:1. Tarsal claw smooth.

LEGS: On the anterior legs all segments with uniformly granulate surface except the metatarsi and tarsi. Tiny granulations on proximal region of metatarsus (Fig. 8). On the posterior legs the



Abbreviations: a.g. arculi genitales; a.o. anal operculum; ch. chelicera; g.a. genital aperture; m.p. manducatory part of palp; m.c. manducatory part of coxa I; st. sternum; t.o. tracheal opening.

TABLE 1: LEG MEASUREMENTS IN MM OF *N. capricornia* ♂ AND (—)

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
Palp	0.22 (0.22)	0.34 (0.34)	0.20 (0.22)	0.28 (0.26)	—	0.30 (0.30)	1.34 (1.34)
Leg I	0.18 (0.18)	0.56 (0.56)	0.34 (0.32)	0.40 (0.36)	0.24 (0.24)	0.46 (0.44)	2.18 (2.10)
II	0.16 (0.16)	0.44 (0.42)	0.26 (0.22)	0.32 (0.30)	0.22 (0.20)	0.42 (0.40)	1.82 (1.70)
III	0.16 (0.16)	0.38 (0.38)	0.24 (0.24)	0.34 (0.30)	0.24 (0.22)	0.36 (0.34)	1.72 (1.64)
IV	0.22 (0.24)	0.50 (0.50)	0.32 (0.32)	0.36 (0.36)	0.22 (0.26)	0.22 0.20 (0.38)	2.04 (2.06)

metatarsi have granulate surface. Tarsal claws smooth. Tarsus I deeper than other tarsi with ventral pad of short hairs. Tarsus IV bipartite. Proximal segment longer than wide, 1.56:1, with dorsal spur distally (Figs. 9, 10).

DESCRIPTION OF FEMALE

Body length 2.20mm, cephalothorax width 1.14mm, abdomen width 1.24mm; chelicera basal segment 0.60, second segment 0.84mm.

This is like the ♂, with the following exceptions. There are no projections of tergite 8 so that the posterior margin of the abdomen is rounded. Tergite 9 is entire and tucked under ventrally to lie behind the anal operculum; anal scopula absent (Fig. 11). Genital aperture is longer than in ♂ and just wider than long, 1.11:1. The arculi genitales are much shorter in front of the genital aperture than in ♂ and the aperture almost abuts coxae III (Fig. 12). The aperture is partly covered posteriorly by an anterior extension of the second abdominal sternite. Tarsus IV is undivided and without a dorsal spur (Fig. 13).

DISCUSSION

The other three *Neopurcellia* spp. are from New Zealand. Of these *N. minutissima* (Forster 1948, pp. 115–6) is the only species that has a ventral spur on the palpal trochanter of both sexes as in *N. capricornia*.

N. capricornia differs from *N. minutissima* in having the second segment of the ♂ chelicera distinctly longer than the basal (1:1.40) whereas in *N. minutissima* they are almost equal (1:1.01). The proximal segment of ♂ tarsus IV is longer than wide whereas in *N. minutissima* it is as long as wide. The dorsal spur on this segment is much blunter than in *N. minutissima*. In his review of the relationships of the Sironinae, Juberthie (1970) places more importance on non-adaptive characters such as the extent

of granulation on leg segments, the cheliceral teeth, and the structure of the ovipositor and penis than previous authors have done. As only two specimens (♂, ♀) of *N. capricornia* were collected, no limbs were removed for detailed examination and the genital organs were not dissected.

It is interesting to note that *N. capricornia* ♂ and ♀ were found in the same litter sample (38 × 45cm plastic bag) of 14 samples collected at Finch Hatton. They were the only cyphophthalmids found in over 200 samples from rainforests of eastern Australia. The two Australian species, *Rakaia woodwardi* Forster 1955 and *N. capricornia* have both been found in tropical Queensland in contrast to the other Southern Hemisphere species all of which are from temperate regions.

ACKNOWLEDGMENT

I am grateful for the support of the Interim Council of the Australian Biological Resources Study which funded the survey of rainforests during which *N. capricornia* was found.

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FIGS. 1–10: ♂ *Neopurcellia capricornia*. 1, body, dorsal; 2, tergites 6–8, postero-dorsal; 3, posterior segments showing composition of corona analis, postero-ventral; 4, body, ventral; 5, arculi genitales and genital aperture; 6, chelicera; 7, palpal trochanter, femur; 8, anterior cephalothorax and leg I, lateral; 9, leg IV; 10, leg IV, proximal tarsal segment with dorsal process and gland opening.

FIGS. 11–13: ♀ *Neopurcellia capricornia*. 11, corona analis; 12, arculi genitales and genital aperture; 13, leg IV, metatarsus and tarsus.



A NEW SPECIES OF *EUASTACUS* (DECAPODA: PARASTACIDAE)
FROM NORTH QUEENSLAND

RONALD MONROE
Queensland Museum

ABSTRACT

Euastacus robertsi sp. nov., from Mt Finnigan, near Cooktown, NE.Q., is described. This species resembles *E. fleckeri* except in colouration, carpal spination, and its triangular rostrum.

The genus *Euastacus* was revised by Reik (1969) to include twenty-seven species, of which only one, *Euastacus fleckeri* (Watson, 1935), was found north of the Mary River, SE.Q. *Euastacus fleckeri* is known from the drainage of Mt Spurgeon and Mt Lewis, near Mt Molloy, NE.Q. Recent field work has yielded a new species from the peak of Mt Finnigan, 80 km north of Mt Spurgeon (Fig. 1).

***Euastacus robertsi* sp. nov.**
(Plate 19, figs. A-G)

MATERIAL EXAMINED

HOLOTYPE: Queensland Museum W5323, ♂, 1050 m, Horan's Creek, Mt Finnigan National Park, NE.Q., coll. 27.xi.1975, L. Roberts, R. Monroe, G. Ingram.

PARATYPES: W5324, 7 ♂♂, 11 ♀♀, same data as holotype.

DIAGNOSIS

Euastacus with an acute triangular rostrum; one large, and two to three small, lateral tubercles on the metopic plate; an accessory row of tubercles on the outer surface of each finger; three to four mesial spines on the carpus; a row of five to seven weak spines along the distero-ventral margin of the carpus, and a spine (the strongest) ventro-mesially.

DESCRIPTION OF HOLOTYPE

Total length (rostral tip, posterior edge of telson) 108 mm.

Cephalothorax: 47.5 mm long, 23.5 mm wide. Cephalic part (28.5 mm long) with numerous blunt tuberosities laterally, glabrous dorsally; rostrum acute (6.0 mm long, 5.5 mm wide at base), sides straight, 3 blunt spines on each raised margin, a

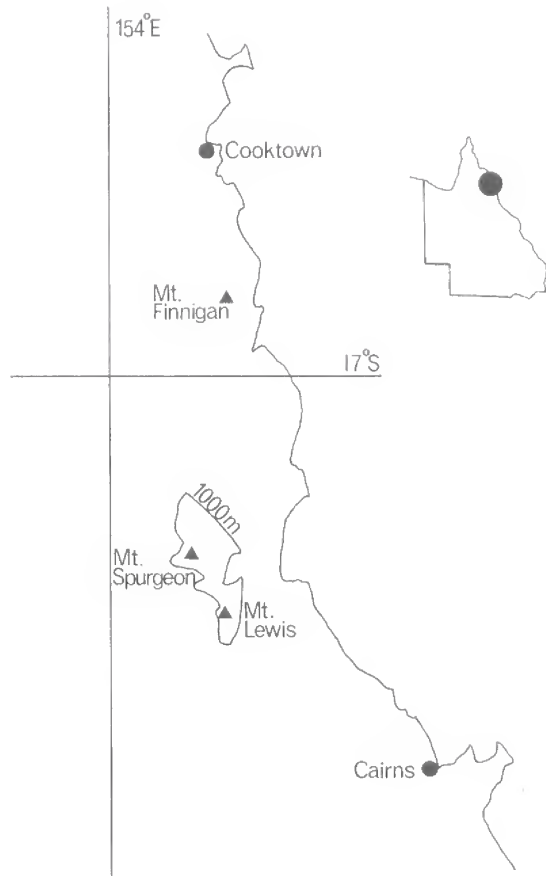


FIG. 1: Locality map, Mt Finnigan, Mt Spurgeon, and Mt Lewis, Queensland.

shallow groove medially runs back into the cephalothorax; post orbital ridge short (3 mm), grooved, with hair tufts, no spine at anterior end, a longer (8 mm) row of punctations mesially; interantennal spine 2.25 mm \times 1.5 mm, straight sided, with 3 small spines at tip; metopic plate smooth, with very sparse short hairs, 11.5 mm wide, lateral wings of metopic plate with 1 large and 2 (left) or 3 (right) small tubercles, shortest length of wings 3.0 mm. Thoracic part with sparse short hairs; areola (19 mm \times 6 mm) with 2 longitudinal rows of short hairs; branchiostegites with numerous small round tuberosities, no spines; sternal keel emarginate between first and second pereopod, straight between second and third, and convex between third and fourth pereopods.

Abdomen: With sparse short hairs; the second pleura with a row of 5 tubercles, the third with 1 spine, laterally; the telson with a lateral spine on each margin; endopodite of uropod with a lateral and medial spine, the exopodite with a central spine, with a row of teeth on each side, and a lateral spine, at the junction of the calcified and membranous parts.

Antenna I: Outer flagellum (17 mm) exceeds inner (15 mm).

Antenna II: Flagellum 71.5 mm long; basal spine prominent, antennal scale with a spine apically, reaching the distal end of the peduncle, expanded mesially.

Third Maxilliped: A spine laterally at apex of ischium, exopod exceeds ischium.

First Pereopod, right (left): Merus, 21 (20) mm long upper edge with a row of 6 (6) small spines on the proximal half; 2 (2) round blunt tubercles dorsally at the distal end, the ventro-mesial margin with 9 (8) spines, the ventro-lateral with 3 (4); a small hair tuft on the dorso-distal margin.

Carpus, 17 (16.5) mm long, a slight depression on the dorsal surface, spination complex. There are 4 (3) strong spines in the mesial row. There is an irregular row of 5 (7) weak spines parallel to the distero-ventral margin, the most mesial of these lying on the mesial margin of the carpus in line with the row of strong mesial spines (giving the appearance of one extra spine in the mesial row). There is a strong ventro-mesial spine adjacent to the mesial row.

Prodopos, 41.5 mm \times 19.5 mm (35.5 \times 17.5); the lateral margin with one complete, and a second incomplete row of blunt spines; the upper surface distolaterally with blunt round tubercles; mesial margin with 7 (7) low blunt spines; cutting edge of fixed finger with 7 (4) spines.

Dactyl, 19.5 (18) mm long; 8 (5) spines on the cutting edge with a row of hair tufts either side of

this; an accessory row of 7 (6) small spines laterally.

Colour in life: Dull blue-purple with a longitudinal red-brown mark dorsally on the carapace and the tips of larger spines.

VARIATION IN PARATYPES

All the paratypes are smaller than the holotype. In the smaller paratypes the sides of the rostrum are convexly angled but otherwise the general morphology is similar to that of the holotype. The smaller tubercles on the lateral wings of the metopic plate are fewer in some specimens, as are the tubercles on the branchiostegites and anterolateral cephalothorax. The spines on the upper edge of the merus are most commonly 6, on one 4 on another 7. The dorso distal tubercles are 2 except in one paratype where only 1 is present. Spines on the ventromesial margin are from 5 to 9, on the ventrolateral 3 except in one case where 4 are present. There are 3 or 4 strong spines mesially on the carpus, most commonly 4. The strong ventromesial spine is, in one specimen, so mesial as to be almost one of the mesial row. In all other cases it is quite separate. The row of weak spines on the ventral surface varies from 2 to 5, the most mesial (in line with the row of strong mesial spines) being absent in some specimens, and the disposition of the remainder is often quite irregular.

Spines on mesial margin of prodopos are 5 to 7, most commonly 6, teeth on the cutting edge of the fixed and moveable fingers are very variable in number and distribution. The accessory spine row laterally on the dactyl has fewer spines in the paratypes, and in very small paratypes (< 20 mm carapace length) is present only as a ridge.

DISCUSSION

E. robertsi is known only from Mt Finnigan, above about 1000 m. It is found in streams and pools where it either burrows in the bank or makes use of natural crevices for shelter. All specimens of the type series were taken during the day from under rocks or in beds of leaf litter. Most burrows seen had one or two entrances, though some may have had more. At night *E. robertsi* was seen just inside burrow entrances with the antennae and large chelae protruding.

E. robertsi is easily distinguished from all species except *E. fleckeri* in having the largest ventral carpal spine well back from the anterior margin of the carpus. It is distinguished from *E. fleckeri* by the shape of the rostrum (rounded U-shape in *E. fleckeri*, acute triangular in *E. robertsi*), the colour (azure blue with red tips to spines and fingers for *E. fleckeri* and as described above for *E. robertsi*), and

the carpal spination. *E. fleckeri* has an oblique row of 3 strong spines on the ventral surface of the carpus, *E. robertsi* has the arrangement described above.

ACKNOWLEDGMENTS

The permission of the National Parks and Wildlife Service to collect in Mt Finnigan National Park is gratefully acknowledged. Without the guidance and assistance of Mr L. Roberts, for whom the species is named, the type series would not have been collected. The field work was

conducted during a joint Queensland Museum–Australian Museum survey of rainforests funded by the Australian Biological Resources Study. Mr B. Campbell, Queensland Museum, gave helpful advice in the preparation of this paper. Mr A. Easton, Queensland Museum, prepared the photographs for the plate.

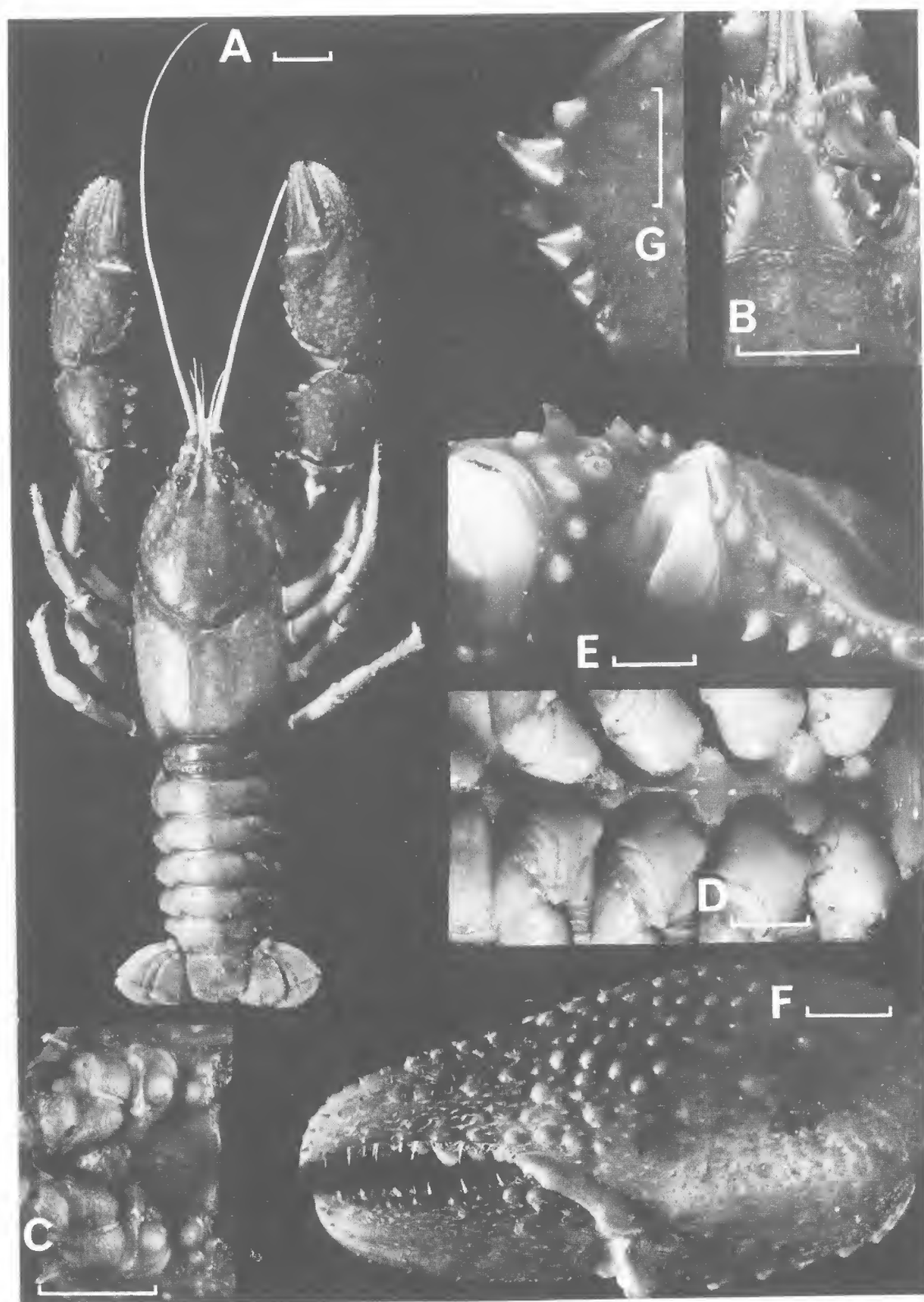
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PLATE 19

Euastacus robertsi sp. nov.

- FIG. A: Dorsal view.
FIG. B: Rostrum and anterior cephalothorax.
FIG. C: Metopic plate and interantennal spine.
FIG. D: Sternal keel.
FIG. E: Ventral view, merus and carpus, right first periopod.
FIG. F: Dorsal view, prodopus and dactyl, right first periopod.
FIG. G: Dorsal view, mesial spine row, merus, right first periopod.
Scales: Fig. A = 1·0 cm, Figs. B-G = 0·5 cm.





ANTECHINUS SWAINSONII (WATERHOUSE, 1840), THE DUSKY MARSUPIAL
MOUSE, AN ADDITION TO THE MAMMAL FAUNA OF QUEENSLAND

S. VAN DYCK
Queensland Museum
and
P. OGILVIE
Queensland National Parks and Wildlife Service

ABSTRACT

Six *A. swainsonii* collected from a variety of vegetation types (elevation 780–1000 m) within Lamington National Park and two National Parks on the Springbrook Plateau between 1966 and 1975 are the first specimens to be recorded from Queensland. Aspects of behaviour and physiology suggest the possibility of a male die-off after a July–August breeding.

Antechinus swainsonii has been recorded from Tasmania, South Australia, Victoria and New South Wales. The most northerly record (Australian Museum) is from the Guy Fawkes district (30° 25' S, 152° 20' E) near Armidale, New South Wales. Calaby (1970) notes that *A. swainsonii* was not found in the upper Richmond and Clarence Rivers region although suitable habitat occurs there.

Four adult males from Lamington National Park, an adult female from Warrie National Park and a juvenile male from National Park 752 Numinbah, collected between 1966 and 1975, are the first records from Queensland. Five are registered in the collection of the Queensland Museum (JM834–6, JM1594–5) and one is lodged in the collections of the National Parks and Wildlife Service (registration number N11506).

Lamington National Park (19,851 ha) in the south east corner of Queensland encloses a section of the McPherson Range and adjacent northern spur ranges. Vegetation types present include rainforest, beech forest, wet sclerophyll forest, open eucalypt forest and mallee heath. Average annual rainfall is 1525–1650 mm.

Warrie National Park (624 ha) lies partly on the Springbrook Plateau and also encloses the headwaters of the East Branch of Little Nerang Creek. The Nimmel Range forms the eastern boundary of the Park. Vegetation types include rainforest, wet sclerophyll forest, open eucalypt forest and patches of secondary forest resulting

from logging or clearing prior to National Park gazettal.

National Park 752 Numinbah (198.7 ha) encloses a narrow strip of land along the McPherson Range at the southern end of the Springbrook Plateau. The Park extends into Numinbah Valley. Rainforest, antarctic beech forest and secondary forest are represented in the Park. Average annual rainfall on the Springbrook Plateau is 3821 mm.

Cranial, dental and external measurements of adult males are presented in Table 1 and are taken as shown in Archer (1976). Wet measurements were taken from JM835 and N11506. Although our sample size is small, comparison of mean dimensions of the four adult male Queensland specimens with mean dimensions of three adult males from the Guy Fawkes district (Australian Museum specimens M8344, M6007 and Queensland Museum specimen J3809) suggests that the Queensland males are equal to or larger than the north New South Wales males in all measurements taken.

Wet measurements in mm for female (JM1595) and juvenile male (JM1594) are as follows: Basicranial length 22.4, 22.5 respectively; zygomatic width 16.2; —; outside bullae width 12.5, 10.3; inside bullae width 4.4, 3.1; C¹–M⁴ 12.7, —; M¹–⁴ 6.9, —; M¹–³ 5.8, —; R–LM³ 9.5, —; minimal interorbital width 7.9, 6.8; inter-palatal vacuity distance 4.3, —; dentary length 24.0, 17.8; I₁–M₄ 13.9, —; M₁–₄ 7.6, —; M₁–₃ 5.9, —; condyle to angular process 5.9, 4.7; condyle to anterior border of ascending ramus 5.5, 4.3; hindfoot (without

TABLE 1: COMPARATIVE MEASUREMENTS OF QUEENSLAND AND GUY FAWKES ADULT MALE *Antechinus swainsonii* (IN MILLIMETRES)

Measurement	Queensland specimens					Guy Fawkes specimens			
	JM835	JM836	JM834	N11506	Means	M8344	M6007	J3809	Means
Basicranial length	33.6	34.0	33.0	—	33.5	34.0	29.6	30.7	31.4
Zygomatic width	18.6	19.3	19.4	19.5	19.2	20.0	17.2	17.2	18.1
Outside bullae width	13.1	13.2	13.4	13.7	13.3	12.7	—	12.8	12.7
Inside bullae width	4.6	4.7	4.9	5.0	4.8	5.3	—	4.3	4.8
C ¹ - M ⁴	13.4	13.5	13.7	14.0	13.6	13.5	12.7	13.0	13.1
M ¹⁻⁴	7.4	7.4	7.3	7.8	7.5	7.1	7.1	7.5	7.2
M ¹⁻³	6.2	6.2	6.1	6.5	6.2	6.3	6.0	6.4	6.2
R - LM ³	10.1	10.1	10.5	10.0	10.2	10.4	9.8	10.0	10.1
Minimal interorbital width	7.9	8.5	8.1	8.1	8.1	8.0	8.0	8.4	8.1
Inter-palatal vacuity distance	4.1	4.7	4.7	5.1	4.6	3.4	3.1	3.9	3.5
Dentary length	27.5	27.1	26.1	28.0	27.2	27.3	23.4	24.2	25.0
I ₁ - M ₄	16.1	15.3	14.8	16.0	15.5	16.1	14.7	15.2	15.3
M ¹⁻⁴	7.7	7.8	7.8	8.1	7.8	7.9	7.7	8.3	8.0
M ¹⁻³	5.9	6.3	6.0	6.3	6.1	6.3	5.7	6.0	6.0
Condyle to angular process	6.4	6.6	6.6	7.1	6.7	7.2	6.1	5.6	6.3
Condyle to ant. border of ascending ramus	6.7	7.0	6.8	7.0	6.9	7.4	6.3	6.5	6.7
Hind foot (without claws)	23	24	24	25	24.0	24	23	23	23.3
Tail-vent	130	129	131	141	132.7	106	124	95	108.3
Head-body	142	137	145	—	141.3	158	99	131	129.3
Total length	272	266	276	—	271.3	264	223	226	237.7
Ear (from notch)	19	18	18	19	18.5	17	17	—	17.0
Weight (g)	—	—	120	—	120.0	90	—	—	90.0

claws) 20.0, 14.8; tail-vent 94.2, 54.3; head-body 111.2, 60.3; total length 205.4, 114.6; ear (from notch) 16.1, 10.0.

JM836 was trapped (PO) 3 August 1966, in a Perske wire trap (39 × 20 × 16 cm) baited with bacon, in a region of the park known as Dave's Creek Country (28° 13' S, 153° 12' E; elevation 900 m). This is an area of mountain mallee heath, approximately 162 ha in extent, developed on soils derived from rhyolite. It is surrounded by rainforest and wet sclerophyll forest. A prominent trachyte dyke known as Surprise Rock outcrops near the capture site. Plant species present include *Leptospermum lanigerum*, *L. flavescens*, *Banksia collina*, *Leucopogon melaleucoides*, *Callistemon montanus*, *Lepidosperma canescens* and *Eucalyptus codonocarpa* (mallee). Jones (1964) provides a detailed description of the floristics and physical characteristics of the region. The abrupt change from rainforest to mallee heath is closely associated with edaphic factors. At the capture site the heath was dense and formed a continuous canopy. Isolated *E. codonocarpa* emerged to a height of 6–7 m. A ground layer of herbs and sedges was present.

JM835 was trapped (SVD) in rainforest near Binna Burra Lodge (28° 12' S, 153° 11' E; elevation 780 m) in an Elliott collapsible aluminium trap (33 × 10 × 9 cm) on 5 August 1974. The trap was located between the buttress roots of a large fig (probably *Ficus watkinsiana*) adjacent to the road at the Park entrance. The specimen died after two days in captivity. This patch of rain forest contains a number of mature eucalypts (*Eucalyptus microcorys*, *E. grandis*, *E. saligna*, *E. acmenoides*) and brush box (*Tristania conferta*) which suggests that the area was previously wet sclerophyll forest, rainforest species having established probably as a result of changes in the fire regime. A ground cover of ferns is present.

JM834 was captured by hand (SVD) on 26 July 1975, approximately 1 km northwest of O'Reilly's Guest House (28° 13' S, 153° 7' E; elevation 900 m). It was observed at 10.00 a.m. scurrying in the leaf litter of a stand of regenerating rainforest in which the dominant species was *Rhodomertus psidioides*. It ran into a burrow (approximately 75 cm long and 7 cm in diameter), constructed amongst the roots of a sapling and ending blindly in an unlined chamber approximately 7 cm below ground level. This individual was maintained in Brisbane until its death in early October 1975 (Plate 20). Two weeks after capture its urine was found to contain abundant spermatozoa.

N11506 was found dead on a Park walking track by Mrs M. Masson 27 July 1975 approximately 3 km southeast of O'Reilly's Guest House (28° 15' S,

153° 9' E; elevation 1000 m) in mature rainforest. The body had been chewed in half, one foreleg and portion of the abdomen having apparently been eaten by an unknown predator and the head and hind quarters abandoned. The head was brought back by Mrs Masson and the hind quarters collected by one of us the following day. A predator could have carried the specimen some distance to the place where it was finally found. Both dingoes (*Canis familiaris dingo*) and tiger cats (*Dasyurus maculatus*) are present in the area.

JM1594 (juvenile with dP4) was found dead by K. Bade (a National Parks and Wildlife Service officer) on 25 December 1968 in a small patch of antarctic beech (*Nothofagus moorei*) within National Park 752 (28° 14' S, 153° 16' E), elevation 1000 m).

JM1595 was found dead by K. McDonald (another officer of the N.P.W.S.) on a graded walking track, 80 metres south of the point at which the track branches to The Canyon and Twin Falls, in Warrie National Park, approximately 400 m from the park headquarters (28° 13' S, 153° 16' E, elevation 780 m) on 2 May 1971. The collection site was immediately adjacent to an area of tall layered open forest dominated by blue mountain ash (*Eucalyptus oreades*) and New England ash (*E. andrewsii*); associated with these is a dense understory of *Callicoma seratifolia*, a re-growth species whose presence is probably a direct result of earlier logging activities in the area. An area of *Leptospermum* sp. and sedges nearby was also recorded by the collector.

A. swainsonii inhabits rain forest, wet sclerophyll forest, alpine woodlands and heaths (Ride 1970). Wakefield and Warneke (1963) describe some of these habitat types in more detail and record captures from mountainous areas down to sea level. Green (1972) records *A. swainsonii* in Tasmania from beech dominated rainforest and adjacent ecotones; specimens were taken at altitudes ranging from 1000 m to sea level. In southeast New South Wales (Nadgee Nature Reserve) Newsome (1975) obtained high trap captures of *A. swainsonii* in upland heath (elevation 500 m); it was also taken from lowland swamps.

The four Lamington specimens were found in a variety of vegetation types—tall closed-forest (rainforest), closed-forest (regenerating rainforest) and closed-heath (Specht et al. 1974). In each case the projective area of ground covered by the foliage of dominant plants was greater than 70%. This also appears to be the case in habitats described by others for this species. The closed-forest types offer abundant litter and rotting logs. Elevation of capture sites ranges from 780 m to 1000 m. In view

of the extensive trapping carried out by one of us (PO) in the National Park during 1966–67 resulting in only one capture of *A. swainsonii*, it would appear that this species either is trap shy, excluded from traps by other species (cf. Newsome 1975), occurs in localised areas of suitable habitat (cf. Wakefield and Warneke 1963), or some combination of these.

There are insufficient details about the habitat types for the two Springbrook specimens. If JM1594 came from the *Callicoma* regrowth area, this would not appear to conflict with a proposal that *A. swainsonii* is associated with a closed canopy, although it does suggest that this canopy need not necessarily be formed by the dominant vegetative layer. JM1594 was collected in closed-forest (antarctic beech forest). Both collection sites lie within the elevation range of the Lamington captures and average annual rainfall is well in excess of that recorded for Lamington.

In captivity JM834 ate one or two day-old chicken carcasses each night. These were grasped in the mouth, lifted high in the air and bashed from side to side on rocks and the cage sides before being eaten. Burrows were constructed in grass and other plant material supplied on the cage floor. Wakefield and Warneke (1963) note similar burrow construction for *A. swainsonii*.

Later, when placed in a smaller cage containing an exercise wheel, JM834 wore the pads from all its feet and ground off its incisors. After a month it became suddenly moribund, developed an inflamed condition on the left flank, lost flank fur, and died. Ground down incisors, heavily worn pads and loss of flank fur occur in male *Antechinus flavipes* just before death during late September in the Beerwah region (P. Dwyer pers. comm.).

Wakefield and Warneke (1963) found in Victoria that *A. swainsonii* breeds during a restricted period in late winter. In June the testes are at maximum size and the pouch area becomes enlarged in late July. Size of the testes was used as the only external indication of sexual maturity in males. Green (1972) found the Tasmanian subspecies to breed later, and over a more extended period. Newsome (1975) records breeding in Nadgee as starting mid-July.

Considering the combination of deaths in captivity; spermatozoa in the urine, diurnal wanderings, capture of sexually mature males at the same time of the year, and the collection of juvenile JM1594, it is tempting to suggest a yearly breeding cycle and male die-off similar to but a month prior to that proposed by Wood (1970) for *Antechinus stuartii* which also occurs in the capture areas.

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PLATE 20

Antechinus swainsonii JM834, photographed shortly after capture, showing long head, very elongate claws, and small ears characteristic of this species.





THE MACROBENTHOS OF SERPENTINE CREEK

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ABSTRACT

Fourteen transects were sampled for macrobenthos in a habitat of small mangrove-fringed creeks at five periods from August 1972 to November 1973, using an 0.05 m² van Veen grab and 1 mm mesh sieves.

Data on depths, sediments, salinity, and water temperature were obtained. These abiotic data showed marked temporal variation but indicated coarser sediments in midstream sites and those near the mouths of the estuaries. The most offshore sites showed a salinity range of ca 26‰ to 35‰ and the most upstream sites a range of ca 6‰ to 27‰.

Much of the biota can not be identified to the specific level, reflecting the scant attention given to small estuarine systems on the eastern coast of Australia. Ninety-eight taxa were recorded, about half the number present in the adjacent Bramble Bay, and less than a quarter the number from other parts of Moreton Bay.

Recordings of species in samples were highly skewed and most data were transformed using $\log_{10} (N + 1)$. Even after this there was a high proportion of species with 'patchy' high recordings.

From the three dimensional data of species \times sites \times times, by summation, two dimensional matrices of species \times sites and species \times times were derived. Using the classificatory technique of Stephenson, Cook and Raphael (1977) site-groups and their conforming species were derived. Seven such groups were accepted, indicating fairly small scale topographic patterning, and this made conceptual sense in terms of abiotic data. Site-groups at the upper and lower portions of the sampled area showed the noticeably high population densities and low diversities regarded as characteristic of estuarine biotas.

Classification of species \times times results did not produce conceptual sense and it is suggested that intervals between sampling were too long. Nevertheless noteworthy fluctuations in the populations of several species were documented.

Attempts are made to describe species in an ecological terminology developed from temperate experience, but problems over the temporal heterogeneity of non-estuarine situations in local waters suggest that caution is required. Of the commoner species *Apseudes estuarius* is the dominant species in all site-groups except those in or close to Bramble Bay, and approximates to an estuarine endemic species. While *Spisula trigonella* appears as an estuarine endemic on the present data elsewhere it acts as an euryhaline opportunistic species. *Xenophthalmus pinnotheroides* approximates to an euryhaline opportunist.

The present work is an analysis of a study (Campbell, Wallace, and King 1976) which was part of a continuing investigation of the likely ecological effects of extension of the Brisbane Airport. Other investigations related to the airport scheme and relevant to the present work have already been published or are approaching this stage. These include a study of the macrobenthos of

Bramble Bay by Stephenson, Raphael and Cook (1976) covering approximately the same period as the present work. Bramble Bay lies immediately offshore from the present sampling area and is the most relevant of the other studies, but direct comparison of results is not possible because a different sized grab (0.1 m²) was used.

In January 1974, after data had been collected

for the present work and that by Stephenson, Raphael and Cook (1976), the Brisbane region received unusually heavy rainfall which caused one of the worst floods since the area was settled (see Ward 1974). The study area was resampled after the flood, and monthly collections are continuing at two groups of sites in Serpentine Creek. The Bramble Bay project continued without interruption (Stephenson, Cook and Raphael 1977).

Another related project concerns the fish of Serpentine Creek and Serpentine Branch (Stephenson and Dredge 1976). This deals with part of the present study area, over roughly the same period, but deals with a different biota.

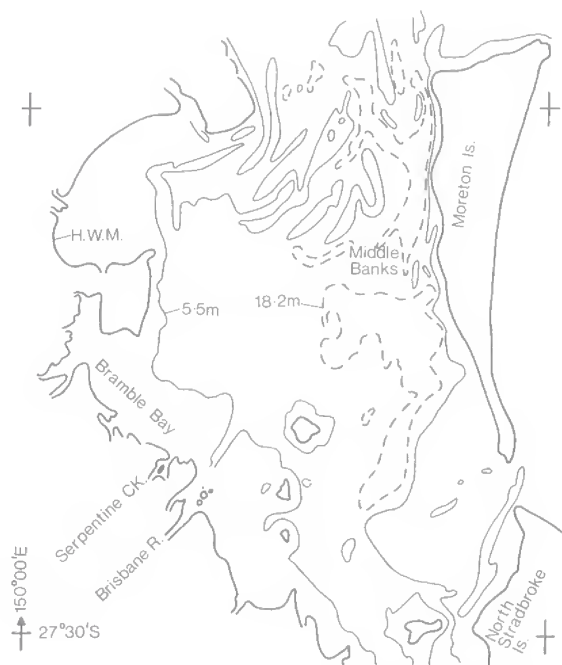


FIG. 1: Map showing localities mentioned in the text.

The present study area (see Figs. 1 and 2) would certainly be affected by major airport extension. The upper portion of Serpentine Creek and the Serpentine Branch would be filled, and input of both fresh and tidal waters to the portions that remain would be greatly reduced. Eventually the system could silt up to the point of almost complete disappearance. Meanwhile Jackson's Creek would carry the diverted drainage with increased scouring by floods and general reduction of salinities in its tidal portion.

The present analysis documents a situation which may cease to exist, and provides some basis for assessing possible changes in Jackson's Creek. The present interest is in 'average' con-

ditions, and also in the fluctuations from average during tolerably normal conditions.

DESCRIPTION OF STUDY AREA

Serpentine and Jackson's Creeks traverse a low-lying area north of the Brisbane River, and enter the southern portion of Bramble Bay. Freshwater drainage into Serpentine Creek is primarily from the 75 km² catchment area of Kedron Brook, which flows from the D'Aguilar Ranges to enter the south branch of Serpentine Creek via Schultz Canal, and also from surrounding airport, farming, and suburban areas which are drained by a number of constructed canals. Freshwater drainage to Jackson's Creek is from the immediately surrounding low-lying area of some 500 ha; its mouth is almost closed at low tide by a shallow bar.

Extensive intertidal sand flats line the foreshore area and the entrances to both creeks. From the mouth of the inlets to the upstream extent of the study area the banks are muddy, and lined with broad belts of mangrove flats and salt marsh. The main mangrove species is *Avicennia marina* var *australasica*, sometimes with an under-layer of *Aegiceras* or *Ceriops* and an occasional specimen of *Rhizophora*. The vegetation of this area is described by Durrington (1977), and the littoral fauna is described by Campbell, Wallace, and King (1976).

SAMPLING PROGRAM

Fourteen transects were chosen at right angles to one or another of the creeks. Three were on Jackson's Creek, four on the Serpentine branch and the remainder on and beyond Serpentine Creek. Three points were sampled on each transect—right bank (facing upstream), mid-stream (deepest portion) and left bank, and this gives 42 sites in all (See Fig. 2). Traverses were either marked with high visibility viscose tape or line-of-sight bearings were recorded. Site relocation errors are about ± 2 m for creek transects, ± 5 m for offshore transects. On each sampling, two catches were made with an 0.05 m² van Veen grab. Catches were sieved on board using 1 mm apertures and one sample comprises the two pooled catches.

It had been intended to sample at regular three-monthly intervals but actual collecting times were: Aug. 1972, Nov. 1972, Feb. 1973, July 1973 and Nov. 1973. These are referred to below as Times 1–5 respectively. Not all sites were sampled on each occasion and details of missing samples are given in Table 1.

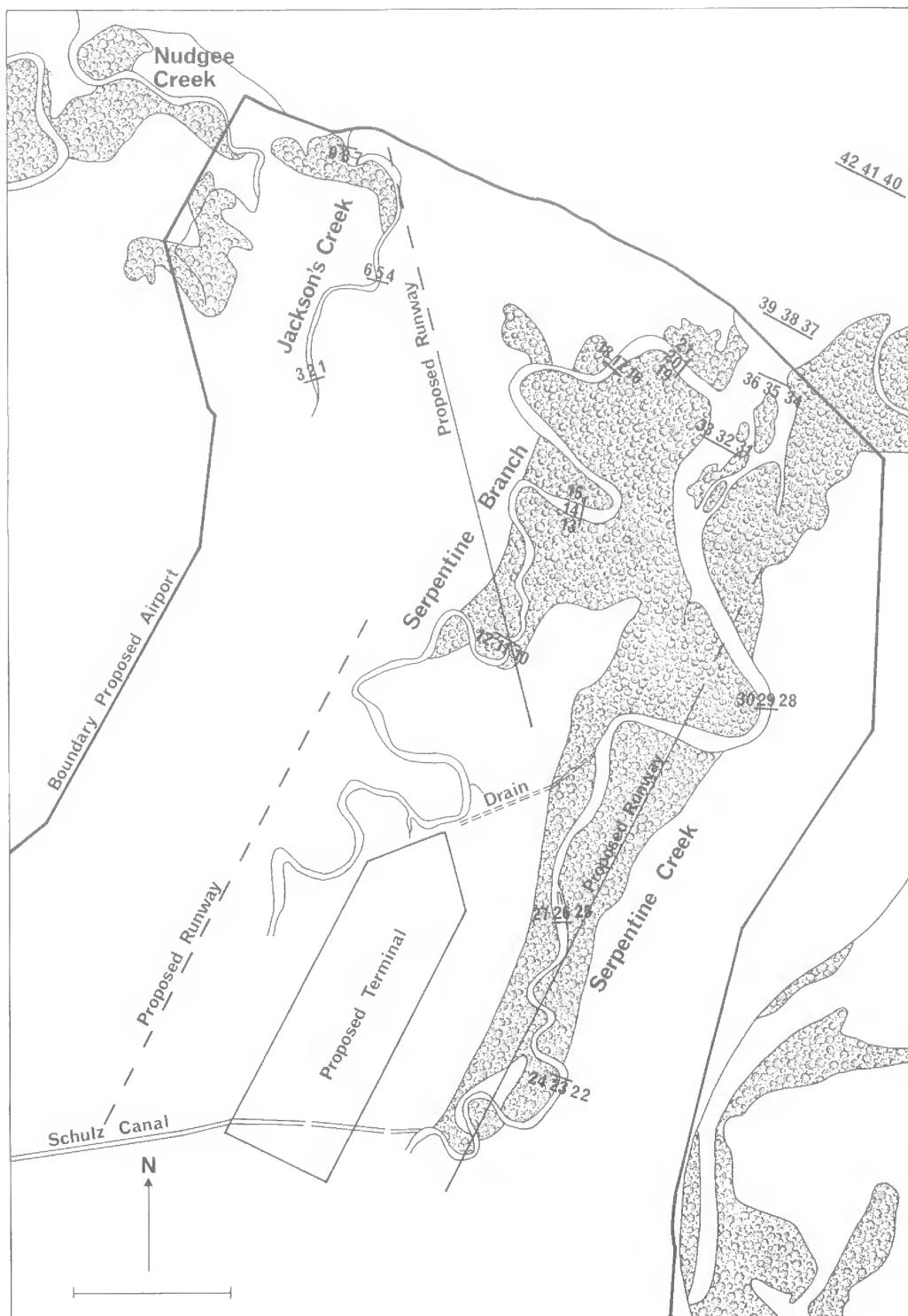


FIG. 2: Map showing the study area and sites sampled.

ABIOTIC DATA

Information on depths, sediments, salinity and water temperature was obtained during the present survey. This has been supplemented by predicted

tidal heights from Tide Tables, Department of Harbours and Marine (1972, 1973); rainfall figures from the Commonwealth Bureau of Meteorology, Brisbane; and hydrographic data from C.S.I.R.O. Division of Oceanography and Fisheries, Cronulla.

TABLE 1: DATA ON SITES SAMPLED

Transect*	Site No.†	Missing times	Mean depth (m)	Observed sediment
Jackson's Creek				
J4	1	—	1.0	s/m
	2	—	2.0	g/s/m
	3	—	1.5	s/m
J3	4	—	1.5	s/m
	5	—	2.0	g/s/m
	6	—	1.0	s/m
J2	7	—	1.0	s
	8	—	2.5	s
	9	—	2.0	s/m
Serpentine Branch				
3B	10	1, 2, 3	2.0	s/m
	11	1, 3	2.0	s/m
	12	1, 2, 3	1.5	s/m
2B	13	—	1.5	s/m
	14	—	2.5	s/m
	15	—	1.0	s/m
1B	16	—	3.5	s/m
	17	—	4.0	g/s/m
	18	—	2.5	s/m
0B	19	1	1.0	s/m
	20	1	3.5	s/m
	21	1	1.5	m
Serpentine Creek				
4	22	2	2.0	m
	23	—	3.5	s
	24	2	1.5	m
3	25	—	1.0	s/m
	26	—	3.0	s
	27	—	2.5	s
2	28	—	2.0	s/m
	29	—	3.5	s/m
	30	—	1.0	s
1	31	—	1.5	m
	32	—	3.0	s/m
	33	—	1.0	s/m
0A	34	1	1.0	g/s/m
	35	1	3.5	g/s/m
	36	1	1.5	g/s
0C	37	1, 3, 4	1.0	g/s
	38	1, 4	2.0	g/s/m
	39	1, 4	1.5	s
0F	40	—	1.5	g/s/m
	41	4	2.0	g/s/m
	42	4, 5	1.5	s/m

* Transect numbers are those used by Campbell et al 1976. See text for explanation of sediment symbols.

† Site numbers for each transect are listed in order: left bank, midstream, right bank (facing upstream).

DEPTHS: All sampling was at approximately high water and depths were recorded. It was impossible with tidal data available to correct these to a common datum, and in Table 1 results are given to the nearest 0.5 m. The alternative was to use data from charts produced in October 1972 for the then Commonwealth Department of Works. This might have occasioned greater inaccuracies due first to difficulties in position location on the chart and secondly to possible depth changes with time.

SEDIMENTS: Sediments from each grab were visually inspected and described in terms of m (mud), s (sand), and g (gravel, shell, wood particles). At times 1 and 2 sediments were collected and analysed for particle size distribution (see Campbell, Wallace, and King 1976). Visual estimates were reasonably compatible with analyses except that mud, as visually estimated, included not only the measured silt-clay fraction ($< \frac{1}{16}$ mm) but also a percentage of the fine sand fraction ($\frac{1}{4} - \frac{1}{16}$ mm). An approximate conversion of visual estimates would be: m = 10% silt + clay; m = 25% silt + clay; s = 60% sand + fine sand; s = 90% sand + fine sand; g = shell, grit, gravel, or wood particles present.

At a given site sediment descriptions changed from time to time. To some extent this could be due to inaccurate relocation of sites on a patchy substrate, but there is also an indication of change with time in that within the estuaries average sediments were predominantly sandy at time 1, muddy at time 3 and approximately equally sand and mud at times 2, 4, and 5. Average site descriptions are given in Table 1.

Certain tendencies are evident in these sediment data: (1) as might be expected the sediments in mid-stream within the estuaries are generally coarser (10/12 cases) than at either bank; (2) sediments containing grit are common at the mouth and beyond the mouth of Serpentine Creek and its branch; (3) near the mouth of Jackson's Creek and outside the mouth of Serpentine Creek the sediments are generally coarser than further upstream.

HYDROGRAPHIC AND RELATED DATA: C.S.I.R.O. Division of Oceanography and Fisheries, Cronulla, surveyed five stations within the present area of

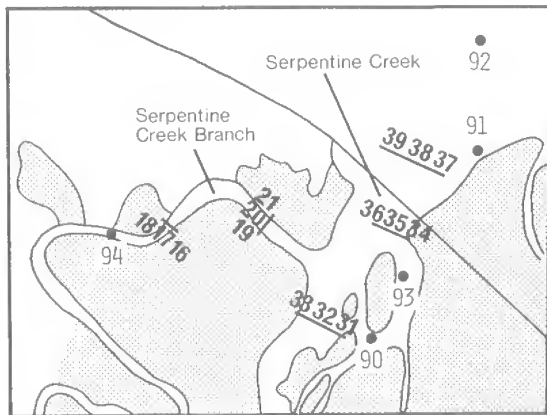


FIG. 3: Map showing hydrographic stations sampled by C.S.I.R.O. (large numerals 90-94) with our sites (bold numerals).

interest. These stations, with C.S.I.R.O. numbering 90-95 were situated as shown in Fig. 3; at each of these, at approximately fortnightly intervals, bottom water was sampled at night-time high water and depth, salinity and temperature were measured. For station 90 the data ran from 26 July 1972 to 4 May 1973, while for stations 91-94 they ran from 28 April 1972 to 4 May 1973. Data for each of these stations over the period 26 July 1972 to 4 May 1973 are given as means and variances in Table 2. One salinity value was extremely low compared with the rest, and a substitute value was used in the calculations (sta. 91; 18 Feb. 1973; 25.5‰ substituted for 15.5‰).

Table 2 shows a gradient from lowest salinity (30.2‰) and greatest variance in the uppermost station (94) to highest salinity (32.06‰) and least variance in the lowermost station (92).

Only station 94 is any appreciable distance within an estuarine system (Serpentine branch) and in tidal and temperature data this station differed

from the remainder, which were almost identical. Station 94 had the greatest tidal amplitude, and temperatures were slightly higher (0.5°C) during the period of rising temperatures from April to February.

Changes in depth, temperature, salinity, and rainfall at the Brisbane Weather Station are shown in Fig. 4. The high level of correlation ($r = +0.86$) between salinity and the summated rainfall for 28 days prior to and including the day of salinity measurement is apparent (Figs. 4C, D).

Campbell, Wallace, and King (1976) recorded bottom salinities at approximately high tide at times 2-5, and temperatures at times 3-5. Results are shown in Fig. 5. Times 2, 3, and 4 show the expected salinity gradient in Serpentine Creek, Serpentine branch and Jackson's Creek. At time 5, Serpentine Creek exhibited the usual gradient but with relatively high upstream salinities; in Jackson's Creek and Serpentine branch the gradient was reversed or non-existent. Rainfall recorded at the Brisbane Weather Station for the 28 day periods prior to times 1-5 is shown in the inset to Fig. 5A.

Temperature gradients were present in the estuaries. At time 3 (Feb. 73) in Jacksons Creek upstream transects were warmer (1-2°C) than downstream transects, but within the Serpentine Creek system Serpentine branch transects were cooler than offshore transects (3°C). At time 4 (July 73) all three sets of upstream transects were cooler (2-3°C), and at time 5 (Nov. 73) all were cooler (1-2°C).

BIOTIC DATA

A total of 98 taxa were recognised in the collections including four which are suspected to be polyspecific. Only one quarter (23) could be identified to the specific level; this reflects the scant

TABLE 2: MEANS AND VARIANCES OF DEPTHS, TEMPERATURE AND SALINITIES AT C.S.I.R.O. HYDROGRAPHIC STATIONS, 26 JULY 1972 TO 4 MAY 1973

Stations (from upper to lower)	Depth (m)		Temp. (°C)		Salinity (‰)	
	Mean	Variance	Mean	Variance	Mean	Variance
Serpentine Branch 94	2.32	0.25	24.02	14.62	30.26	21.94
Serpentine Creek 90	0.78	0.08	23.51	12.74	31.47	11.06
93	0.92	0.07	23.69	13.16	31.55	10.40
91	1.11	0.08	23.60	13.84	31.63	9.23
92	2.13	0.15	23.60	13.84	32.06	6.79

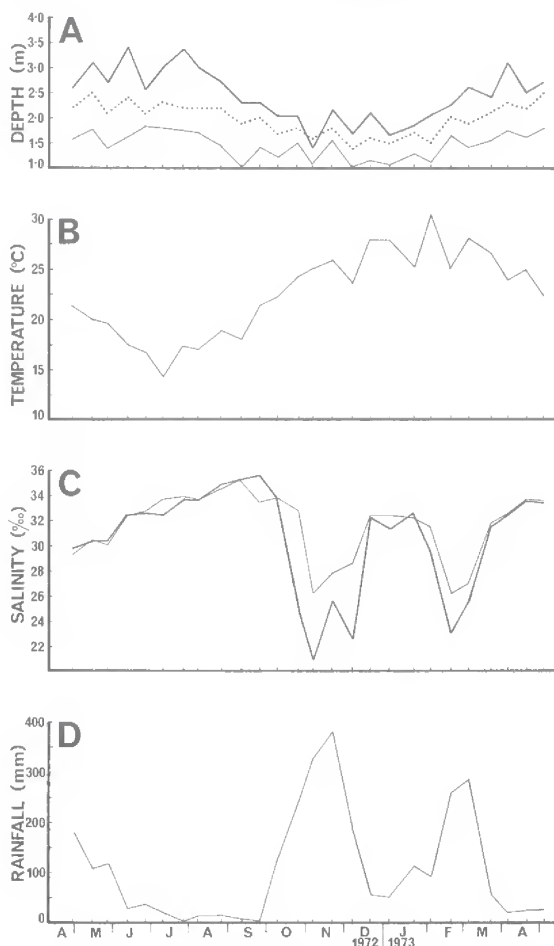


FIG. 4: Hydrographic and related data mostly from C.S.I.R.O. survey. Marks on base-line show times of sampling.

A: Depths. — = Station 94, . . . = predicted high waters at Brisbane Bar, — = mean for stations 91-93.

B: Temperatures. Mean for stations 91-94.

C: Salinities. — = means for stations 91-93, — = station 94.

D: Rainfall at Brisbane Weather Station over 28 days prior to salinity measurements.

attention which has been given in the past to estuarine benthos on the east coast of Australia. The percentages of species in major taxa were: Crustacea 46, Polychaeta 23, Bivalvia 16 and Gastropoda 14. Within the 46% for Crustacea, 19% were Decapoda and 16% Amphipoda. These percentages differ considerably from those of Bramble Bay (see Raphael 1974) in which the dominant groups with percentages were: Polychaeta 39%, Bivalvia 27% and Arthropoda 17%.

The outstanding features of the present data are the large number of amphipod species and the absence of echinoderms and tunicates.

ANALYSES OF DATA

The data form a three-dimensional matrix of 98 taxa (s for species) \times 42 sites (q for quadrats) \times 5 times (t). The easiest way to handle such data is to summate across each dimension in turn and thus derive three two-dimensional matrices. In the present case because data are incomplete, after summation, averages must be used.

The first two-dimensional matrix we consider is derived by compressing the 98 species values to a single value and considering the $q \times t$ matrix of 42 sites \times 5 times. Actually a number of $q \times t$ matrices are considered.

In the above analyses we consider all species, but treat them as anonymous. In the remaining main analyses we reduce the number of species under consideration (see Data Reduction below) but retain specific identities. These later analyses deal with species (s) by sites (q) with data averaged over times and with species (s) by times (t) with data averaged over sites.

ANALYSES OF SITES \times TIMES

Direct summation of numerical recordings of all species gives the number of individuals per sample (N), and this is the numerical equivalent of biomass. Another summation gives the number of species per sample (S), and this is a simple measure of diversity; it is the species density in Hurlbert's (1971) terminology. A further measure of diversity was used, the standardized Shannon diversity (H^1) (see Stephenson, Raphael, and Cook 1976). (Throughout logarithms to base 10 were employed). In the resultant three $q \times t$ matrices containing values of S , N , and H^1 respectively, overall mean values were S 7.68, N 234.8 and H^1 0.46. In each of the three matrices we also obtained a mean value for each site (by averaging over times, maximum number 5) and a mean value for each time (by averaging over sites, maximum number 42); ranges and variances of these means are given in Table 3.

With both S and H^1 values the variance due to sites is about 6 times that due to times, while with N values the ratio is over 12 times. Variance in populations (N) is considerably affected by occasional large values which cause skewing of the data. This is almost eliminated by the transformation $\log_{10}(N + 1)$: thus on the total array with raw values γ_1 (moment coefficient of skewness) was 3.94 and γ_2 (moment coefficient of kurtosis)

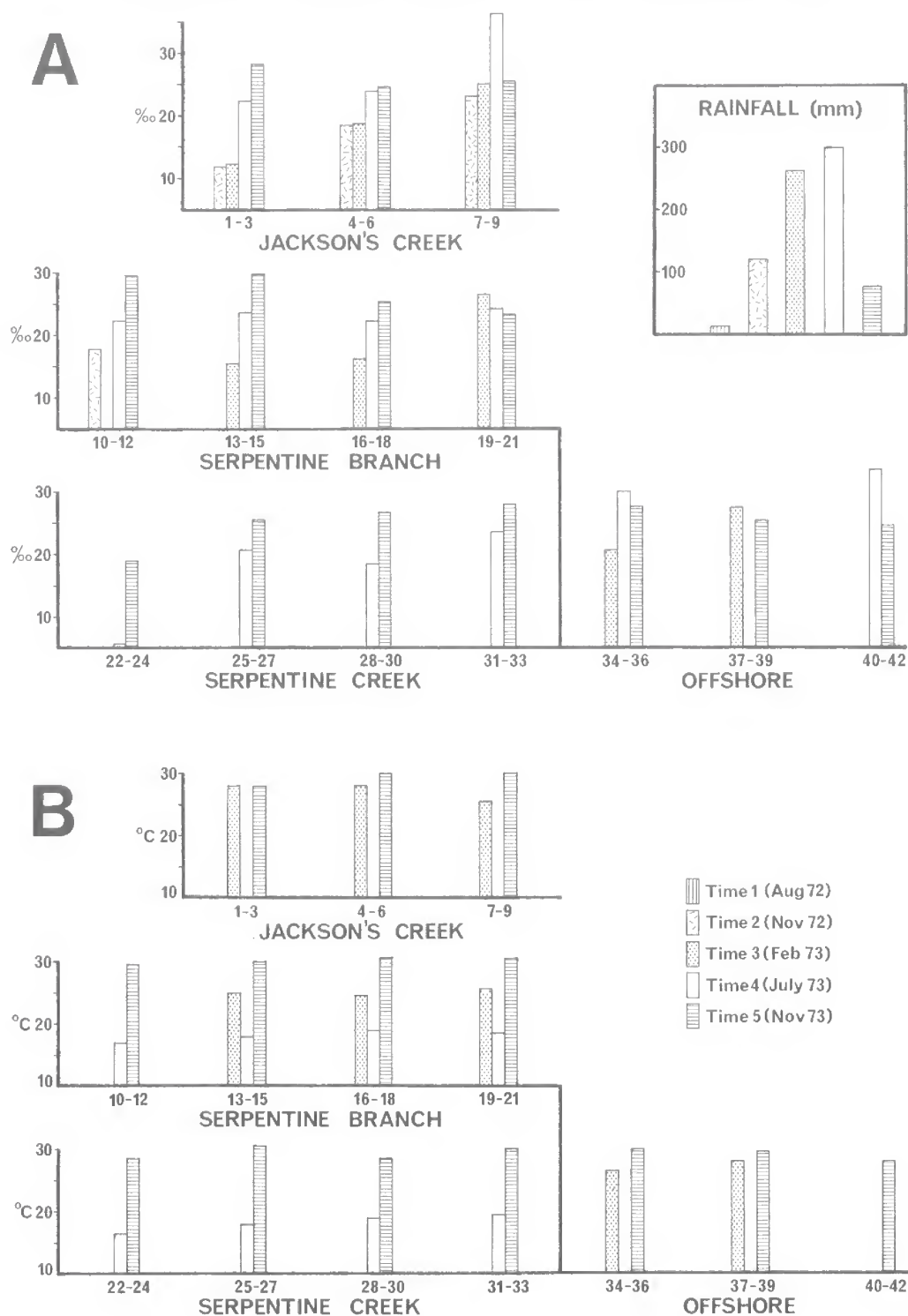


FIG. 5: Hydrographic data recorded at survey sites, times 2-5.

A: Salinities. Inset shows rainfall at Brisbane Weather Station over 28 days prior to times 1-5.

B: Temperatures.

TABLE 3: MEAN SITE VALUES AND MEAN TIME VALUES OF S , N , H^1 , AND $\text{LOG}_{10}(N + 1)$

	Sites		Times	
	Range	Variance	Range	Variance
S	3.2-12.3	6.33	6.50-8.63	0.919
N	13.2-1412.8	79938.0	105.6-315.6	6341.6
H^1	0.12-0.76	0.025	0.38-0.55	0.004
$\log_{10}(N + 1)$	1.04-2.75	0.196	1.68-2.01	0.019

was 20.91; after transformation these became 0.21 and 2.51 respectively. Using transformed numbers the overall mean is 1.83 and variance due to sites becomes about 10 times that due to times (see Table 3).

TABLE 4: MEAN VALUES OF S , $\text{LOG}_{10}(N + 1)$ AND H^1 FOR GROUPED SITES

Site groups	Sites	S	$\log_{10}(N + 1)$	H^1
A				
Jackson's Creek	1-9	6.87	1.58	0.48
Serpentine System	10-36	7.82	1.86	0.47
B				
Serpentine Creek	22-33	6.43	1.83	0.40
Serpentine Branch	10-21	8.46	1.88	0.50

By grouping sites and comparing the mean values of S , N and H in the groups it is possible to reveal patterns in the above data. Apart from comparisons between the main channels we defer this until after sites classification. The first comparison now considered is between sites in the two main drainage systems; Jackson's Creek and Serpentine Creek including its branch. We exclude from the latter sites 37-42 which lie beyond the mouth of the Serpentine system and thus compare sites 1-9 (Jackson's Creek) with 10-36 (Serpentine system). Results are given in Table 4(A), and while the differences are not significant, they suggest that Jackson's Creek has relatively fewer species and fewer individuals than the Serpentine system. The Shannon diversities are the same in the two systems, no doubt because the lower numbers of species and of individuals 'cancel out' in the Shannon formulation.

The second comparison is between the main portion of Serpentine Creek (sites 22-33) and the Serpentine branch (sites 10-21) excluding the shared portion (sites 34-36). Results (Table 4(B)) suggest approximately equal numbers of individuals in the two portions, but with more species and higher diversity in the Serpentine branch.

The relevant times data are given in Table 5. The lowest S and H^1 values are in time 3 (February 1973) which agrees with other local results. Apart from this it is difficult to see patterns in the data, for example times 1 and 4 (August 1972 and July 1973) do not show any overall similarity and neither do times 2 and 5 (Nov. 1972, Nov. 1973). A comparable absence of seasonal patterns was noted by Stephenson, Raphael and Cook (1976) in Bramble Bay.

TABLE 5: MEAN VALUES OF S , $\text{LOG}_{10}(N + 1)$ AND H^1 IN DIFFERENT TIMES

Times	S	$\log_{10}(N + 1)$	H^1
1	8.6	2.01	0.47
2	6.7	1.68	0.48
3	6.5	1.73	0.38
4	8.4	1.82	0.55
5	7.4	1.94	0.41

DATA REDUCTION

For reasons stated variously elsewhere (see Clifford and Stephenson 1975) it is desirable to reduce the number of species under consideration prior to classification of the $s \times q$ or $s \times t$ matrices. We declare an interest in abundance and eliminate species whose abundance in the total sampling was 5 or fewer individuals.

The 53 residual species are given in the Appendix in order of abundance, and the code numbers follow this hierarchy. Subsequent reference to species is mostly by code number, sometimes accompanied by generic name.

PATCHINESS OF DATA

Perusal of the full data shows occasional very high values of certain species in samples. These give bias to all analyses, and already in considering the $q \times t$ data we have effected $\log(N + 1)$ transformations. In the classifications which follow ($s \times q$ and $s \times t$) even with data transformed as above

we may expect that occasional outstanding large values will unduly influence the situation. In conceptual terms these can be regarded as showing patchiness in space and time, and there are two ways in which they can be investigated. The first is in 'precautionary' pre-classification analyses, and the second is after classification has been undertaken.

For pre-classification analyses we use the method employed by Stephenson, Raphael, and Cook (1976). The largest transformed value of a species in all samples is selected, and an analysis of variance is undertaken using this value against the remainder. F values of all species are considered and by adopting an arbitrary F value as a scale we can pinpoint the extremely patchy species and the samples in which they show outstandingly high values. Five times the F value for the 0.001 probability level is taken.

This gives the following as 'extremely patchy' species in sites \times times: 4, 5, 12, 19, 27, 24, 22, 29, 33, 31, 34, 36, 45, 38, 37, 39, 40, 42, 43, 50, 46, 48, 49, 44, 47, 52, 53. These total 28 out of 53 (leaving 25) compared with 25 out of 79 (leaving 54) in the Bramble Bay data. Clearly in the present case we are dealing with much more 'spikey' data.

The examples of space-time patchiness have no especial time concentration, but show a hint of site concentration, four examples occurring in each of the following lower estuary sites: 9, 19, 31, 35 and 38.

CLASSIFICATION

These consider either species (s) by sites (q) or species (s) by times (t). In both cases we use values averaged over the 'suppressed' dimension of the original matrix and transform these using $\log_{10}(N + 1)$. Throughout we are interested in abundance and have two main dissimilarity measures to choose from: the widely used Bray-Curtis measure (see Clifford and Stephenson 1975; Stephenson, Raphael, and Cook 1976); and the unstandardized Manhattan metric which Stephenson, Cook, and Raphael (1977) preferred for impoverished situations and for other reasons. Because the present data includes several impoverished samples the Manhattan metric is used.

Details of the classificatory technique follow those of the above authors and in brief are: (1) for entities (sites or times) Manhattan metric dissimilarity, group-average sorting; (2) for species as above but standardize by totals after transformation. Entity classifications in both cases were truncated at appropriate levels and scrutinised for possible misclassifications and subsequent re-allocations. Subjective judgement was involved in

the truncations (as outlined later), and also in whether or not to re-allocate single entities which appeared as groups; these are general problems of the group-average sorting strategy.

As obtained by the method outlined, species groups were not of great conceptual value. The main reason is that, after standardizing by totals, the less common species have a major role in species classification and yet they occur in such low numbers (and often in such patchy fashion) as to show scant relationship to the entity-groups. If we restrict our interest to those species that characterize entity-groups in a quantified fashion, we eliminate most of the species in the matrix. In the present case this 'wrecks' the species classification produced by the computer, but so few species remain that visual classification is adequate.

Species reduction at this second stage (the first stage was the elimination of species with a total abundance of 5 or fewer) was in two steps. We first eliminated species which did not attain an average population of 1.0 individuals in any of the site-groups under consideration. These comprised the species lowest in the abundance hierarchy and a few at slightly higher levels which approximated to an even spread over the site-groups. In the second step we looked for 'noticeable' differences between recordings in the site-groups taking cognisance of mean values in site-groups and also their variances. As outlined in previous papers (Stephenson and Dredge 1976; Stephenson, Raphael and Cook 1976) there are problems in this procedure. We have used the mechanics of the F test because the outcomes relate closely to those obtained by visual scanning of data. Although we employed $\log_{10}(N + 1)$ transformations of the data to remove the worst of the skewness we appreciate that, because we have classified the data, we have destroyed its randomness and thus the rationale for legitimate use of the test. Hence we refer to this as the 'pseudo F test' and speak of 'noticeable' differences and not 'significant' ones. Transformed values of species recordings were tested using various combinations of site-groups, and usually one site-group against the others. Species were eliminated if the pseudo F value was less than the F value giving 0.05 probability; the residual species hence conform to the site-groups in the terminology of Stephenson, Williams and Cook (1974).

ANALYSES OF SPECIES \times SITES: Results of the classification of sites is shown as a dendrogram in Fig. 6. At the 10 Manhattan unit dissimilarity level there are six groups of very unequal sizes, labelled A-F on the dendrogram base. We consider these in

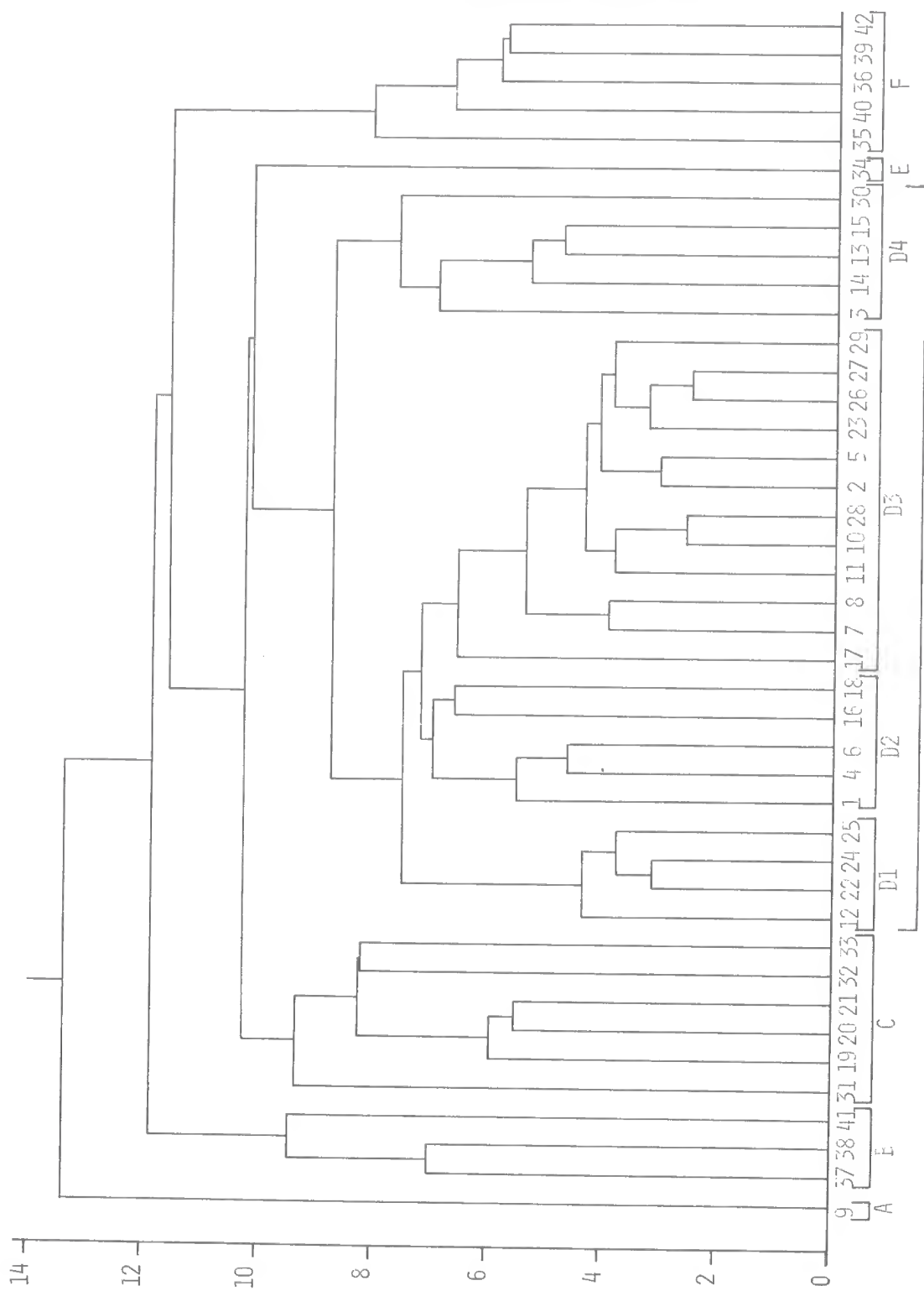


FIG. 6: Dendrogram of site-groups, Manhattan metric dissimilarity $\log_{10}(N + 1)$ data.

the first instance, and deal later with the subdivisions of the largest site-group (D).

Two of the site-groups consist of single sites: site-group A (site 9) and site-group E (site 35). Both are difficult to reallocate to any of the remaining groups. Site 9, near the base of a steep eroding muddy bank at the mouth of Jackson's Creek, is characterized by the following species: 3 (*Xenophthalmus*), 7 (*Laonice*), 15 (*Grandidierella*) and 4 (*Corophium* sp. 1). Of these, two (spp. 7 and 15) were previously noted as showing extreme patchiness in site 9. Site 34, a similar situation at the mouth of the Serpentine Creek system, is mostly characterized by species 7 (*Laonice*).

The species conforming to the main site-groups (B, C, D and F) were arranged in species-groups and the two-way table is given in Table 6. It is evident that the species-groups characterize the site-groups in a clearly interpretable manner. conversely the site-groups can be described as

'communities' in terms of their commonest characterizing species, but because of chronological variations some qualifications are needed as indicated below.

The site-groups show topographic and sedimentary coherence (see Fig. 7). Site groups B (sites 37, 38, 41) and F (sites 35, 36, 39, 40, 42) at or beyond the mouth of the Serpentine system have predominantly grit and sandy sediments. *Spisula* is abundant in both groups. *Xenophthalmus* was common in sites 35 and 36 of area F at time 5; *Urohaustorius*, *Mysella* and acteonid also characterize this area. Area B is characterized by *Corophium*, *Paracorophium*, *Gammaropsis* and *Melita*, but abundance of these varied greatly from time to time. When collection sites were accurately relocated in or near mid-stream these species were most abundant, and site group B is seen as a mid-stream outside group. Sediments were, on average, finer than those of site group F.

TABLE 6: CONFORMING SPECIES (ARRANGED IN SPECIES-GROUPS) CHARACTERIZING THE MAIN SITE-GROUPS WITH MEAN NUMBERS PER SAMPLE IN THE SITE-GROUPS

Species group	Species (code no.)	Site Groups			
		B	C	D	F
I (most in B)	<i>Corophium</i> (4)	130.7	0	0.1	0.5
	<i>Paracorophium</i> (5)	77.7	0	0.4	0.1
	<i>Grandidierella</i> (15)	7.0	0.2	0.8	3.0
	<i>Gammaropsis</i> (19)	8.8	0	0.2	0
	<i>Melita</i> (29)	3.5	0	0	0
II (most in C)	<i>Xenophthalmus</i> (3)	0	53.4	0.2	11.5
	<i>Laonice</i> (7)	0	3.9	1.4	0.1
	<i>Sanguinolaria</i> (10)	0	9.7	1.4	1.8
	capitellid (11)	0.4	6.8	1.7	1.1
	<i>Owenia</i> (12)	0	8.2	0.1	0.2
	<i>Armandia</i> (23)	0	1.0	0.3	0
	<i>Tellina</i> (25)	0	1.5	0.1	0
	<i>Lumbrinereis</i> (28)	0.1	1.2	0	0.4
III (most in D)	<i>Apseudes</i> (1)	0	59.5	170.2	0.2
	<i>Eriopisa</i> (8)	0	1.7	5.5	0.2
	<i>Haploscoloplos</i> (9)	0	0.2	4.1	0
	<i>Arthritica</i> (17)	0	0	2.2	0
	<i>Ceratonereis</i> (18)	0.1	0.4	1.3	0.2
IV (most in F)	<i>Urohaustorius</i> (13)	0	0	0.8	9.5
	acteonid (14)	1.2	3.4	0	5.5
	<i>Mysella</i> (16)	0.5	1.3	0.2	6.6
V (co-equal B and F)	<i>Spisula</i> (2)	265.5	9.6	6.2	294.3

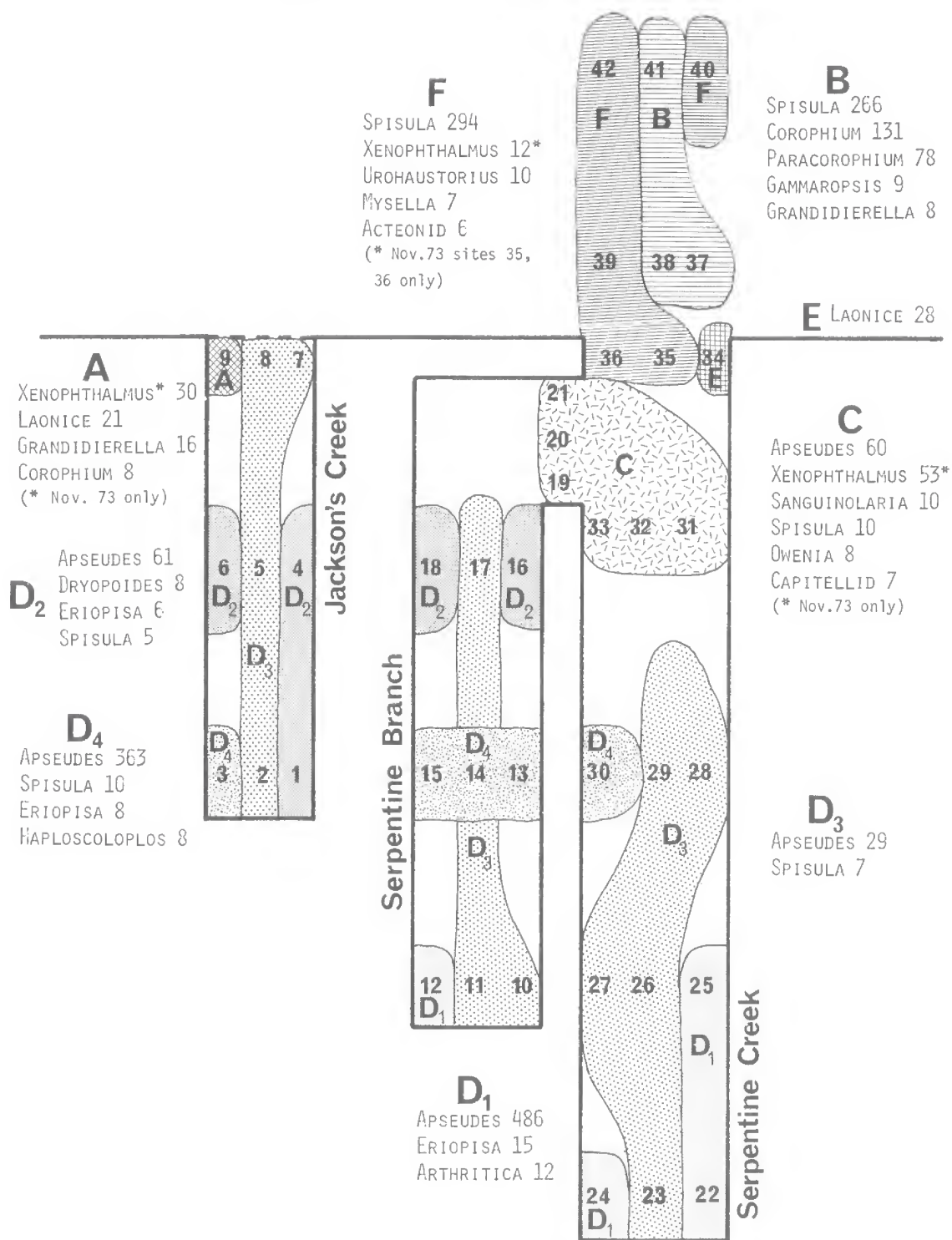


FIG. 7: Schematic diagram of survey area showing site groups and abundance of commoner species ($n > 4$) in each site group.

TABLE 7: CONFORMING SPECIES (ARRANGED IN SPECIES GROUPS) CHARACTERIZING THE SUBORDINATE SITE-GROUPS D1–D4, WITH MEAN NUMBERS PER SAMPLE IN THE SITE-GROUPS

Species group	Species (code no.)	Site-Groups			
		D1	D2	D3	D4
(i) (most in D1)	<i>Arthritica</i> (17)	12.0	0	0.6	0.2
	<i>Diala</i> (40)	1.4	0	0	0
(ii) (most in D3)	<i>Sanguinolaria</i> (10)	0	0.3	2.7	0.6
(iii) (most in D4)	<i>Grandidierella</i> (15)	0	0.2	0	4.3
	<i>Ceratonereis</i> (18)	1.5	1.0	0.7	3.0
	<i>Laternula</i> (20)	0.1	0.5	0.1	1.5
	<i>Australonereis</i> (21)	0	0.1	0.2	1.7
	sabellid (22)	0.2	0.7	0.1	1.6
(iv) (almost coequal most D1 and D4)	<i>Apseudes</i> (1)	486.4	61.2	29.1	363.2
(v) (least in D1)	<i>Spisula</i> (2)	0.2	4.7	7.1	10.4
	<i>Dryopoides</i> (16)	0.2	7.7	3.0	6.6
	<i>Laonice</i> (7)	0.2	3.4	1.1	1.0
	<i>Haploscoloplos</i> (9)	0.1	4.6	2.7	8.2
(vi) (least in D3)	<i>Eriopisa</i> (8)	14.5	5.9	1.3	8.1
	capitellid (11)	2.5	2.2	0.3	3.8

Site group C (sites 19–21, 31–33, lies just inside the mouth of the Serpentine Creek system, where sediments are variable but mostly muddy. It is characterized by the occasional occurrence of *Xenophthalmus* in large numbers (time 5 only, $N = 186$) and the remaining species of group II. *Apseudes* is common ($N = 59.5$) but not as abundant as in group D. Site group C has no counterpart in Jackson's Creek, possibly because of the smaller size of that creek and because its mouth is largely closed by a shallow sand bar.

Site group D contains 27 sites, comprises all of the 'within estuary' sites, and can be resolved into four subordinate site-groups shown as D1, D2, D3 and D4 on the base of Fig. 6. The species characterizing these site-groups are arranged in species-groups in Table 7. There are possible ambiguities in this arrangement, for example species-groups (iv) and (vi) have much in common.

All the subordinate site-groups are dominated by *Apseudes* (sp. 1), but the mean numbers per sample are different and the dominance is most

marked in D1 and D4. The subordinate species are different in each case. In D1 they are *Eriopisa* (sp. 8) and *Arthritica* (sp. 17), in D2 they are *Dryopoides* (sp. 6) and *Eriopisa* (sp. 8), in D3 *Spisula* (sp. 2) and in D4 *Spisula* (sp. 2), *Haploscoloplos* (sp. 9) and *Eriopisa* (sp. 8). Site-group D4 is positively characterized by the largest number of species (five) and site-group D1 negatively characterized by the largest number (four).

The subordinate site-groups again show topographic coherence (Fig. 7). *Site-group D1* comprises sites 12, 22, 24 and 25. These are on the upper traverses of Serpentine branch and Serpentine Creek and all are bank sites with depths of 1–2 m and sediments exclusively or predominantly of mud. *Site-group D4* comprises sites 3, 13, 14, 15, 30. These are in the middle traverses of Serpentine Branch and Serpentine Creek and the upper traverse of Jackson's Creek. All are bank sites except 14, which is the mid point of a traverse where the stream was broad, slow flowing, with almost uniform depth and sediment throughout its width.

Site-group D2 comprises sites 1, 4, 6, 16 and 18. These are restricted to Jackson's Creek and the Serpentine branch, and all are bank sites at approximately similar distances from the coastline. The sediments are either sand and mud or sandy mud: *Site-group D3* comprises sites 2, 5, 7, 8, 10, 11, 17, 23, 26, 27, 28 and 29. These are widely distributed throughout the length of the estuarine portions of the sampling area. Most are midstream sites (2, 5, 8, 11, 17, 23, 26 and 29). Of the remainder, 27 although nearest the bank is the deepest site on its transect and represents maximum stream flow; 28, on the outward sweep of the creek is also well within the main stream flow; 10 is a deep bank site in a narrow portion of the creek; and 7 is a very sandy site near the mouth of Jackson's Creek which would also be subject to some stream action. Except for site 28 the sediments are predominantly sandy.

In summary then, excluding the two aberrant sites at the mouths of Jackson's and Serpentine Creeks, the site groups recognised are:

- (a) Outside, away from main stream bed (F)
- (b) Outside, within main stream bed (B)
- (c) Mouth (C)
- (d) Estuarine within main stream bed, eroding substrate (D3)
- (e, f, g) Estuarine away from main stream bed, depositing substrate, which is divided into three sections, upper estuary (D1); mid estuary (D4) and lower estuary (D2).

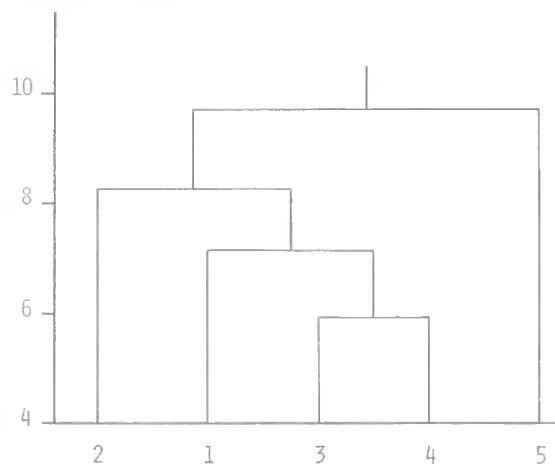


FIG. 8: Dendrogram of time-groups, Manhattan metric dissimilarity $\log_{10} (N + 1)$ data.

ANALYSES OF SPECIES \times TIMES: Using data averaged over all sites, the result of the classification of times is shown on Fig. 8. There is no close grouping of the comparable seasons viz. times 1 and 4, and times 2 and 5, and the closest grouping of times 3 and 4 is sequential. This tendency for sequential rather than seasonal groupings was noted by Stephenson, Raphael and Cook (1976) in their work at Bramble Bay over roughly the same period.

Times were grouped in almost every possible combination to obtain conforming species but

TABLE 8: CONFORMING SPECIES (ARRANGED IN SPECIES-GROUPS) CHARACTERIZING TIMES, WITH MEAN NUMBERS PER SITE AT EACH TIME

Species group	Species (code no.)	Times				
		2	1	3	4	5
I (most in times 2 and 1)	<i>Paracorphium</i> (5)	14.8	5.3	0	1.5	0
	<i>Haploscoloplos</i> (9)	3.0	9.0	1.5	2.2	1.5
	<i>Gammaropsis</i> (19)	0.6	3.0	0	0	0
II (most in time 4)	<i>Xenophthalmus</i> (3)	0	0	0.3	0	38.8
	<i>Owenia</i> (12)	0.1	0.1	0.1	0.1	5.9
	acteonid (14)	0	0	0.6	0.3	4.0
III (least in time 2)	<i>Apseudes</i> (1)	30.6	124.3	250.2	124.3	78.4
	<i>Spisula</i> (2)	14.8	49.1	19.0	78.4	157.3
IV (least in time 1)	<i>Laonice</i> (7)	6.9	0	3.0	1.5	2.2
V (least in time 3)	<i>Dryopoides</i> (6)	2.2	9.0	0	6.9	2.2

without noticeable success. Hence times are taken as separate entities. In Table 8 they are listed in dendrogram order and the conforming species are arranged in species-groups. Only two of the species listed give any indication of seasonal repetition and these are *Apseudes*, species 1 (low in times 2 and 5) and *Dryopoides*, species 6 (high in times 1 and 4).

RELATIONSHIP OF $q \times t$ DATA TO $s \times q$ DATA: Having derived site-groups by considering their specific components, we now compare the following within the different 'communities'—average number of species per sample (S), average population of all species per sample (N), and average individual Shannon diversity per sample (H^1). The equivalent exercise on time-groups is not pursued because clear time-groups are not apparent in the data.

TABLE 9: MEAN VALUES PER SAMPLE OF S , N AND H^1 IN SITE-GROUPS (EXCLUDING THOSE OF SINGLE SITES)

Site group	Sites in Site-group	S Value	N Value	H^1 Value
B	37, 38, 41	5.7	485.9	0.34
C	19, 20, 21, 31, 32, 33	10.3	172.1	0.62
D1	12, 22, 24, 25	5.2	516.3	0.20
D2	1, 4, 6, 16, 18	8.3	101.8	0.53
D3	2, 5, 7, 8, 10, 11, 17, 23, 26, 27, 28, 29	5.0	53.4	0.45
D4	3, 13, 14, 15, 30	8.2	416.6	0.42
F	35, 36, 40, 42	8.0	372.7	0.42

The relevant data contained in Table 9, show a significant negative correlation (-0.83) between N and H^1 using the Spearman rank correlation coefficient.

Site-group D3 is noteworthy in having the lowest sample populations and the fewest species. Site-group D1 is also noteworthy with the highest sample populations, almost as few species, and the lowest diversity. Site-group C has the highest diversity and most species.

DISCUSSION

The main purpose of the present work was to analyse data which attempted to document a situation which is likely to disappear. There were some shortcomings in the information available to us, particularly in relation to abiotic data. To have obtained adequate data upon depths and sediments in this labile habitat would have required more extensive topographic and sedimentary surveys than were possible with resources available. The

existing sediment data show the expected differences between sites with generally coarser sediments in midstream than near the banks and again as one moves downstream. The hydrographic data indicate that at the sites furthest offshore in the present survey there was a temperature range of ca 14.3°C to 30.4°C and a salinity range of ca 26‰ to 35‰ ; of the sites furthest upstream there was a temperature range of ca 14°C to 30°C and a salinity range of ca 6‰ to 27‰ , with salinity closely dependent upon the rainfall of the previous month.

The temporal variation in abiotic data recorded at each site should be stressed. Changes in salinity, depth, sediment, and temperature were so great that often the only common attribute of a given site at time x and the same site at any other time was its geographical location.

Knowledge of the specific composition of the biota is also noteworthy incomplete. This again reflects the general absence of comparable studies in the benthos of the smaller estuarine systems on the eastern coast of Australia. The only relevant work available prior to the present survey was a study of the dredged macrobenthos near the mouth of the Brisbane River (Hailstone 1972). Again the species list was incomplete. Since then Campbell *et al.* (1974) have given a preliminary report on the benthos in nine estuaries in south-eastern Queensland, using similar techniques to those in the present work. Again most of the biota was not identified to the specific level. More recently Boesch (MS) has given a preliminary account of his 1972–73 study of 10 sites extending nearly 70 km upstream from the mouth of the Brisbane River; again identifications are incomplete.

The number of taxa obtained in the present study (98) is about half the number obtained by Raphael (1974) in Bramble Bay, but is about half as many again as the 64 which Campbell *et al.* (1974) obtained in nine local estuaries. It should be noted that this last survey was carried out some while after the devastating floods of January 1974. Stephenson, Cook and Newlands (MS), with somewhat more intensive collecting, obtained ca 450 species in the Middle Banks region of Moreton Bay, and roughly the same number were obtained by Stephenson, Williams and Cook (1972) south of Peel Island in Moreton Bay.

In all the local benthic surveys made by a grab, data have been skewed due to occasional occurrences of very high recordings of many of the species, and this has been allowed for in part by transforming the data using $\log(N + 1)$. Following Stephenson, Raphael and Cook's (1976) 'patchiness' technique, extremely high recordings of

species in their sites \times times occurrences were isolated. The proportion of these 'patchy' species is considerably greater in the present study (28/53) than that in Bramble Bay (25/79).

Turning to broader issues, if we exclude purely faunistic collecting the underlying purpose of macrobenthic sampling is to reveal trends, patterns, or groupings within the data. The scale of patterns which is revealed will depend upon the scale of the sampling. Thus within Moreton Bay and using approximately square grids Poiner (1974) has shown site-groups in benthic samples taken at 6 m apart in work north of Peel Island; Stephenson, Williams and Cook (1974) working south of Peel Island showed groups in sites ca 0.5 km apart; while Stephenson, Raphael and Cook (1976) obtained them in Bramble Bay with sites ca 1 km apart. In the present work there were two scales of sampling, with transects ca 1 km apart aimed at longitudinal (upstream-downstream) patterns and at distances from ca 10 to 100 m apart aimed at transverse (cross-river) patterns. The site-groups which were obtained (Fig. 7) show that purely longitudinal sampling would not have been adequate in the present situation.

Although it might be considered inadvisable to average species \times sites data over all times when dealing with such a labile habitat as an estuary, particularly in the present instance where only 5 times were available, our justification for having done this can be found in the results. The site-groups that were generated appear conceptually sound in relation to topography and average abiotic parameters.

We have recognized seven site-groups in the present study and clearly each occupies a relatively small area. As indicated this may partially reflect original preconceptions as revealed by the spatial aspects of the sampling programme, but this is not the entire picture. The spacing of sites produced topographic sense and this justifies the preconceptions; however the relative absence of chronological sense in the data contradicts the temporal preconceptions regarding the area.

It appears that patchiness in the data has gone close to making meaningless the times \times species classification. Present results show negligible seasonal repetition in the biota and little similarity between consecutive times. These conclusions agree with the general tendencies, albeit better documented, which Stephenson, Raphael and Cook (1976) obtained in Bramble Bay. The present results suggest, in general, that there were insufficient times collected and that the intervals between samplings were too long to produce a meaningful classification of times \times species data.

Selected sites in Serpentine Creek are currently being sampled on a more frequent basis.

Reverting to the spatial situation, we suggest that the small scale topographical patterns are a real phenomenon. Elsewhere it has been hinted that subtropical benthos may have smaller scale area patterning than that of temperate habitats (Stephenson, Williams and Cook 1974; Clifford and Stephenson 1975). It seems that the present patterns are an estuarine manifestation of this phenomenon.

The study closest to the present in locale and general approach was that of Boesch (MS) who investigated the macrobenthos of the Brisbane River for almost a year beginning in 1972. Only near-bank sites were sampled, and at distances of ca 6 km apart. While this sampling strategy involved ten samplings along the length of the estuary against a maximum of seven in the present case, it is clear that small scale patterns would not be revealed. Boesch's numerical approach differed from our own and he rejected site-groupings. The rationale for considering groupings of data has been detailed at length elsewhere (Clifford and Stephenson 1975).

General concepts from estuarine literature suggest that in estuaries populations are high, but diversities are low. It is true that certain of the extreme upper estuarine sites form a site-group (D1, sites 12, 22, 24, 25) with the highest populations obtained in the survey and with the fewest species and lowest standardized Shannon diversity. We presume that the stress factors here are associated with periodic dilution. The next most populous and least diverse site-group is B (sites 37, 38, 41) in the lowest portion of the estuary. We presume that here the stress factors are associated with tidal scour. In general the middle estuary has lower populations, and higher diversities than noted above, but within this area the site-groups show no clear relationships between populations, diversities and topography.

From our early analyses we suggest one important relationship between these three aspects: the Serpentine system as a whole is more populous than Jackson's Creek. If the former is filled in, it will be of interest to determine whether the latter will retain even its present low populations when additional freshwater drainage is diverted into it.

In terms of time, lowest populations were in time 2 (Nov. 1972) and highest in time 3 (Feb. 1973). Both coincide with periods of salinity reduction and hence there is no easy 'explanation' of the results. It should be noted that both are also approximately the inverse of the situation in the more open waters of Moreton Bay (see for example

Stephenson, Williams and Cook, 1974). Until fuller data on time changes are available further discussion of these data is premature.

In the recent benthic literature there are attempts to place species in a single ecological category. The work of Grassle and Grassle (1974) gives excellent examples and categorizations of opportunistic species, and Boesch (MS) uses the following descriptive terms: stenohaline marine, euryhaline marine, euryhaline opportunist, and estuarine endemic. Local work upon *Spisula*, one of the common species in the present survey, suggests that simple categorization is an oversimplification. *Spisula* is often an abundant species in the shallower waters of Bramble Bay (Stephenson, Raphael and Cook 1976) and forms a *Spisula* 'community'. Based on this it could be described as 'euryhaline marine (shallow water)'. Because it does not conform to time in the present survey (see Table 8) it could be described as 'estuarine endemic'. Because after the severe flood of early 1974 it dominated extensive areas of Bramble Bay (Stephenson, Cook and Raphael 1977), as regards the postflood situation it would become 'euryhaline opportunistic'.

Most of the descriptive terms in current use derive from experience of temperate macrobenthos. Past studies in Moreton Bay show that virtually all the commoner species show marked fluctuations in numbers, with both seasonal and annual components (Stephenson, Williams and Cook 1974; Stephenson, Raphael and Cook 1976). The same is true in unpublished studies of the Middle Banks region of Moreton Bay, which is relatively uninfluenced by near-land changes (Stephenson, Cook and Newlands MS). When the biotas of non-estuarine situations approximate to being in a state of flux, it is difficult to relate estuarine species to any non-estuarine basis. If simple descriptive terms are required, the single term 'transient' covers almost all cases.

On a species by species basis there are certain similarities between Boesch's (MS) work and our own, and certain differences. Boesch describes *Apseudes* as an estuarine endemic and it is the dominant species in all our site-groups except those within or close to Bramble Bay. In our work it

showed marked temporal changes, (see Table 8) but apparently did not in Boesch's. Boesch included *Grandidierella* as a dominant estuarine endemic but in our work it was concentrated in the lower estuarine sites and never dominant. Similarly *Ceratonereis* in our study was never dominant and characterized only a small mid-estuarine site-group. *Marphysa* and *Notomastus* were listed by Boesch as estuarine endemics but are equally non-estuarine endemics, both occurring in Bramble Bay, with the former common on foreshores at Stradbroke Island (Stephenson 1967) and the latter common in the deeper waters of Moreton Bay (Stephenson, Cook and Newlands MS). Two other species listed by Boesch as dominants from the Brisbane River (*Owenia* and *Prionospio*) also extend widely to the Middle Banks area of Moreton Bay (Stephenson, Cook and Newlands MS).

In the present work the closest approximation to an euryhaline opportunist is *Xenopthalmus* which is a transient dominant or co-dominant in the lower estuary (site-groups A and C) and less of a transient co-dominant in the shallower waters of Bramble Bay (Stephenson, Raphael and Cook 1976). It was not listed by Boesch (MS) amongst his 37 most frequent species.

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Mr Peter Davie provided invaluable support in preparing the data for analysis and in drafting graphs and histograms. We also thank Mr Stephen Cook for preparing site maps and dendrograms.

APPENDIX

Species from Serpentine Creek benthos with indications of their systematic positions. Only SPECIES WITH ≥ 5 individuals are listed; code numbers are in hierarchical order of abundance.

Code No.	Species	No. of individuals collected
1	<i>Apseudes estuarius</i> Boesch	(Tanaidacea, Apseudidae) 21293
2	<i>Spisula trigonella</i> Lamarck	(Bivalvia, Mactridae) 11962
3	<i>Xenopthalmus pinnotheroides</i> White	(Decapoda, Pinnotheridae) 1662
4	<i>Corophium</i> sp. 1	(Amphipoda, Corophiidae) 1266
5	<i>Paracorophium</i> sp.	(Amphipoda, Corophiidae) 781
6	<i>Dryopoides</i> sp.	(Amphipoda, Corophiidae) 711
7	<i>Laonice</i> sp.	(Polychaeta, Spionidae) 688
8	<i>Eriopisa</i> sp.	(Amphipoda, Gammaridae) 675
9	<i>Haploscoloplos</i> sp.	(Polychaeta, Orbiniidae) 606
10	<i>Sanquinolaria donacioides</i> (Reeve)	(Bivalvia, Gariidae) 482
11	capitellid	(Polychaeta, Capitellidae) 457
12	<i>Owenia fusiformis</i> Delle Chiaje	(Polychaeta, Oweniidae) 289
13	<i>Urohaustorius</i> sp.	(Amphipoda, Haustoriidae) 286
14	acteonid	(Gastropoda, Acteonidae) 222
15	<i>Grandidierella</i> sp.	(Amphipoda, Corophiidae) 216
16	<i>Mysella</i> sp.	(Bivalvia, Montacutidae) 202
17	<i>Arthritica helmsi</i> (Hedley)	(Bivalvia, Erycinidae) 193
18	<i>Ceratonereis erythraeensis</i> Fauvel	(Polychaeta, Nereidae) 180
19	<i>Gammaropsis</i> sp.	(Amphipoda, Isacidae) 105
20	<i>Laternula tasmanica</i> (Reeve)	(Bivalvia, Laternulidae) 103
21	<i>Australonereis ehlersi</i> (Augener)	(Polychaeta, Nereidae) 78
22	sabellid	(Polychaeta, Sabellidae) 72
23	<i>Armandia</i> sp.	(Polychaeta, Opheliidae) 63
24	<i>Polinices</i> sp.	(Gastropoda, Naticidae) 63
25	<i>Tellina cf. deltoidalis</i> Lamarck	(Bivalvia, Tellinidae) 61
26	<i>Paraphoxus</i> sp.	(Amphipoda, Phoxocephalidae) 56
27	<i>Nassarius ellana</i> (Iredale)	(Gastropoda, Nassariidae) 51
28	<i>Lumbrineris</i> sp.	(Polychaeta, Eunicidae) 51
29	<i>Melita</i> sp.	(Amphipoda, Gammaridae) 42
30	<i>Sergestes</i> sp. ? spp.	(Decapoda, Sergestidae) 34
31	<i>Mesanthura</i>	(Isopoda, Anthuridae) 32
32	peneid sp. ? spp.	(Decapoda, Penaeidae) 30
33	<i>Ilyograpsus</i> sp.	(Decapoda, Grapsidae) 26
34	<i>Macrophthalmus</i> sp. ? spp.	(Decapoda, Ocypodidae) 24
35	<i>Nephtys australiensis</i> Fauchard	(Polychaeta, Nephtyidae) 22
36	nereid	(Polychaeta, Nereidae) 21
37	<i>Acteocina fusiformis</i> (Adams)	(Gastropoda, Acteonidae) 20
38	<i>Cerceis</i> sp. ? spp.	(Isopoda, Sphaeromidae) 18
39	<i>Marphysa</i> sp.	(Polychaeta, Eunicidae) 16
40	<i>Diala</i> sp.	(Gastropoda, Cerithiidae) 16
41	<i>Magelona</i> sp.	(Polychaeta, Magelonidae) 16
42	<i>Westwoodilla</i> sp.	(Amphipoda, Oedicerotidae) 14
43	spionid 2	(Polychaeta, Spionidae) 13
44	oedicerotid	(Amphipoda, Oedicerotidae) 10
45	<i>Modiolus</i> sp.	(Bivalvia, Mytilidae) 9
46	dexaminid	(Amphipod, Dexaminidae) 9
47	polychaete 1	(Polychaeta) 9
48	<i>Ringicula</i> sp.	(Gastropoda, Ringiculidae) 8
49	rissoinacean	(Gastropoda) 8
50	epitonid	(Gastropoda, Epitoniidae) 6
51	mesodermatid	(Bivalvia, Mesodermatidae) 6
52	<i>Corophium</i> sp. 2	(Amphipoda, Corophiidae) 6
53	<i>Callanaitis</i> sp.	(Bivalvia, Veneridae) 6

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THE EFFECT OF A MAJOR FLOOD ON THE MACROBENTHOS OF BRAMBLE BAY QUEENSLAND

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ABSTRACT

The macrobenthos of Bramble Bay, which may be affected by proposed extensions to Brisbane Airport, was influenced by a severe flood in Jan. 1974. The benthic study involved two study periods—preflood (June 1972 to Dec. 1973) and postflood (Mar. 1974 to Mar. 1975), with the former already published (Stephenson, Raphael and Cook 1976). Hence the present work evaluates effects of the flood upon a known biota.

Salinities were reduced to at least 24‰ in the area of sampling, and the affected period was prolonged by rainfall associated with a cyclone in Mar. 1974. A transient cover of soft silt occurred after the flood. Sites were grouped by their sedimentary compositions in separate analysis of preflood and postflood data, using clustering technique previously applied to sites/species. Sediment site-groups after the flood showed a complex mosaic of areas and there was an overall increase in muddiness.

The biotic data (preflood and postflood) form a 3D matrix with the main interest in the time axis. Data were derived on the average number of individuals per site (n), average number of species per site (s), and average standardised Shannon diversities per site (d), in each of the times. Diversities were lower after the flood but not significantly so, s values were significantly lower almost throughout, n values were originally significantly lower and finally significantly higher.

Flood effects on separate sites were evaluated by comparing n and s values in various times. In one or another postflood period significant changes occurred in 26/27 sites for n data and 25/27 sites for s data. Overall population effects were greater, with many sites showing higher populations in late postflood than in preflood times.

Flood effects on the 74 most abundant species, were evaluated species by species in terms of populations and areas of distribution. Thirty-six of these species, mostly low in the abundance hierarchy, showed no 'significant' effects. The others showed effects variously categorised for example as v. transient decreases (5 spp.), and 'permanent' decreases (7 spp.), transient increases (5 spp.), and 'permanent' increases (2 spp.). Increases were mostly in areas occupied, rather than site populations, with the commonest species (*Spisula*) increasing from 6.9 to 25 sites.

Investigations were made of changed site-species patterns, and involved hierarchical classifications of species \times sites matrices over selected times viz. preflood, early postflood and late postflood. The technique followed Stephenson, Raphael and Cook (1976) except that the Manhattan metric dissimilarity measure was now used. Preflood there is an inshore site-group characterised by *Spisula*, *Xenophthalmus*, *Terebellides*, *Pupa* etc.; an intermediate depth grouping with *Anadara*, tunicates and an oyster, and an offshore group with *Placamen*, two species of *Amphioplus*, *Theora lata* etc.

In early postflood four sites formed a 'near-rivers' group with *Spisula* markedly dominant, followed by *Pupa* and *Parcanassa*; three sites formed an offshore group with two species of *Amphioplus* and *Theora lata*, and 20 sites with an impoverished biota were weakly characterised by *Anadara*.

In late postflood 22 sites formed a *Spisula-Parcanassa* community, reflecting the spread of these species into the previously 'scarified' area. Two small offshore site-groups were characterised by more species than in early postflood.

A tentative conceptual model of benthic changes in the area is proposed based on the assumption of occasional severe flooding. The effects of the present natural events are likely to be much more obvious than those caused by the proposed airport enlargement.

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Extensions of Brisbane Airport if effected will involve extensive filling of Serpentine Creek and increased drainage through Jackson's Creek. It is possible that these may affect the biota of the adjacent area of Moreton Bay, viz. Bramble Bay (see Fig. 1). Two studies of the macrobenthos of Bramble Bay were planned, the first being before the construction and in the nature of a 'base-line' study. From this it was hoped that predictions could be made of the effects of airport extension. The second proposed study, after construction, would evaluate the actual effects.

Twenty-seven sites, *c.* 1 km apart, were selected in Bramble Bay, and these were sampled for macrobenthos every three months beginning June

1972 (see Fig. 2). Duplicate catches were made by an 0.1 m² van Veen grab and sieved through 1 mm apertures; the two catches were pooled to give a 'sample'.

Heavy rainfall in the catchment of the Brisbane River caused extremely heavy flooding in Jan. 1974 (see Ward 1974). Samples from seven pre-flood times were available and when the eighth set was obtained, *c.* two months after the flood, it was evident that the benthic biota had suffered a marked decline. Just after this collection was made there was further heavy rainfall associated with a cyclone and as shown later, this may have prolonged the adverse effects due to the flood. Sampling continued (from 18 Mar. 1974 to 12

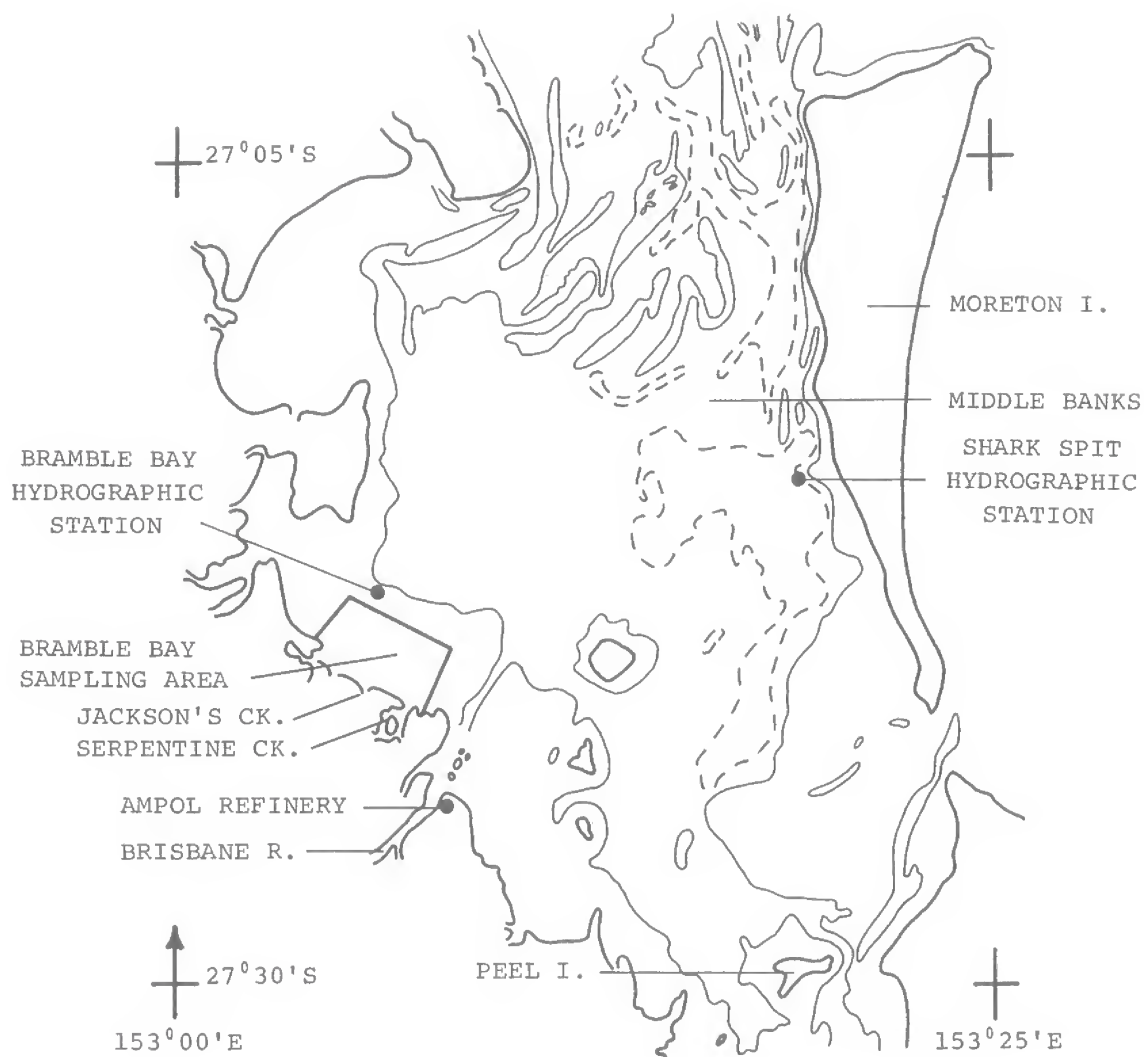


FIG. 1: Map of Moreton Bay showing sampling area and locations mentioned in the text.

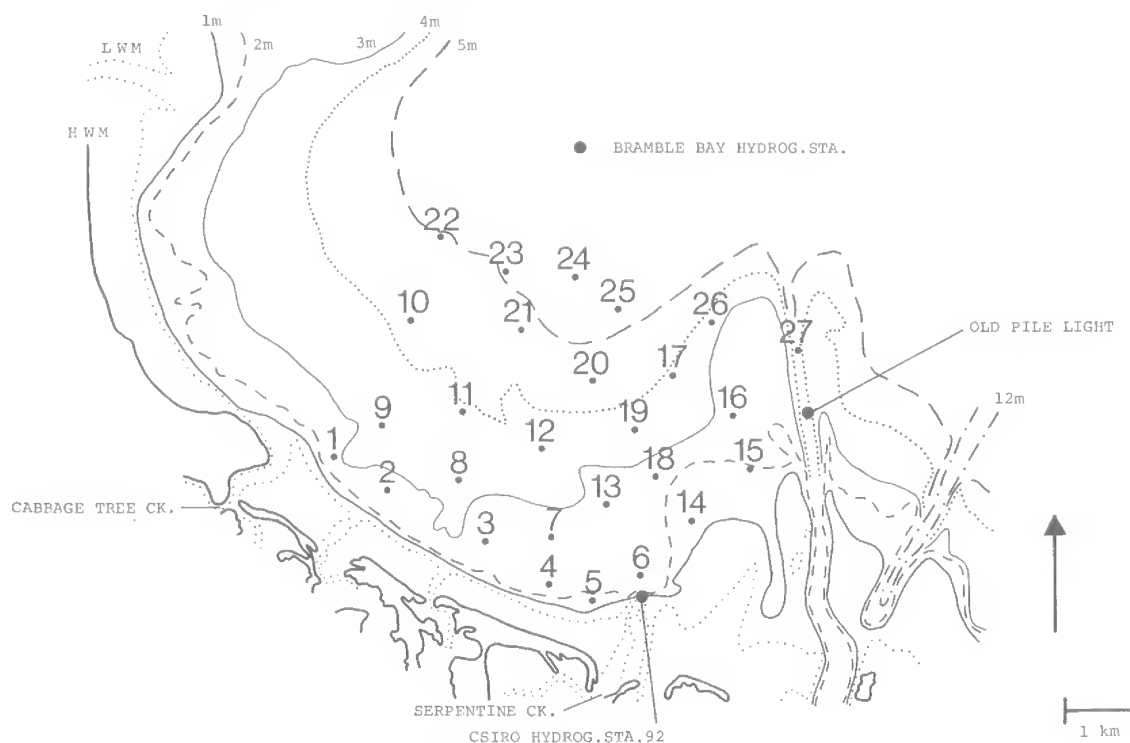


FIG. 2: Positions of sampling sites, CSIRO hydrographic stations, etc. in the Bramble Bay region.

Mar. 1975) until there was clear evidence of biotic recovery. The preflood situation has been documented by Stephenson, Raphael and Cook (1976), and we now consider the postflood situation and relate it to the reasonably normal preflood 'base-line'.

The extensive preflood data permits an unrivalled opportunity to quantify the effects of the flood and cyclone. The analyses of these data are also of applied value and raise the possibility of a later comparison between the effects of a man-made disturbance (airport construction) with natural ones.

Abiotic and biotic data are treated in separate sections in the account which follows, with methods in their relevant sections.

ABIOTIC DATA

DEPTHS: Preflood depth data are given by Raphael (1974) and Stephenson, Raphael and Cook (1976). These data are repeated here on Fig. 2. During the first postflood collection of biotic data (March 1974) it was noted that on the eastern side of the study area (sites 15, 16) depths had decreased by as much as 1.5 m. This was attributed to settlement of material scoured by the flood from

the Brisbane R. At the time of writing there has been no official resurvey of depths in the area.

SALINITY: Two hydrographic studies were undertaken by the CSIRO Division of Fisheries and Oceanography, one at roughly fortnightly intervals over the period Apr. 28th 1972 to May 4th 1973, and another at monthly intervals from Aug. 1972 with data available up to Feb. 1975. One locality in the first study (CSIRO No. 92), near the mouth of Serpentine Ck, is close to our site 6 and monthly averages of salinity at that locality are plotted on Fig. 3A.

The more extensive study involved measurements at different water depths at several localities in Moreton Bay. Those of interest are: Bramble Bay, $27^{\circ}18'S$, $153^{\circ}06'E$, ca 3 km NW. of our site 22, the most NW. of our sites; near Ampol Refinery (mouth of the Brisbane R.), $27^{\circ}25'S$, $153^{\circ}09'E$, ca 6 km from our site 15, and Shark Spit $27^{\circ}17'S$, $153^{\circ}22'E$. Initially we considered salinities in the deepest water sample at each locality (c. 5 m, 11 m and 29 m respectively) as being those most relevant to the benthos. The Brisbane R. samples were less variable than those at Bramble Bay, and because the shallower water at the Brisbane R. would be in more direct communication with Bramble Bay, an intermediate depth (c. 6 m) was also considered.

There were some gaps in the data (see Fig. 3A) but two continuous periods each of a year were available for study viz. Aug. 1972 to July 1973 and Oct. 1973 to Sept. 1974.

The benthic sampling area lies between two of the hydrographic stations and by taking intermediate values from Table 1 we can assume an average salinity in the preflood year of *c.* 32.5‰.

TABLE 1: SALINITIES (PARTS PER 1000) MONTHLY SAMPLES AT FOUR HYDROGRAPHIC STATIONS

Station	Preflood year (Aug. 72–July 73)			Postflood year (Oct. 73–Sept. 74)		
	mean	range	variance	mean	range	variance
Bramble Bay ca 5 m	32.76	27.9–34.94	5.23	30.27	24.3–33.5	10.21
Nr. Ampol Refinery ca 6 m	32.34*	30.1–34.76*	2.79*	29.69	24.8–33.8	5.91
Nr. Ampol Refinery ca 11 m	32.94	30.5–35.14	2.42	30.16	26.2–33.8	4.36
Shark Spit ca 29 m	34.50	33.13–35.33	0.55	33.70	32.0–35.08	1.32

*Values for Nov. 1972, Feb. 1973 not available.

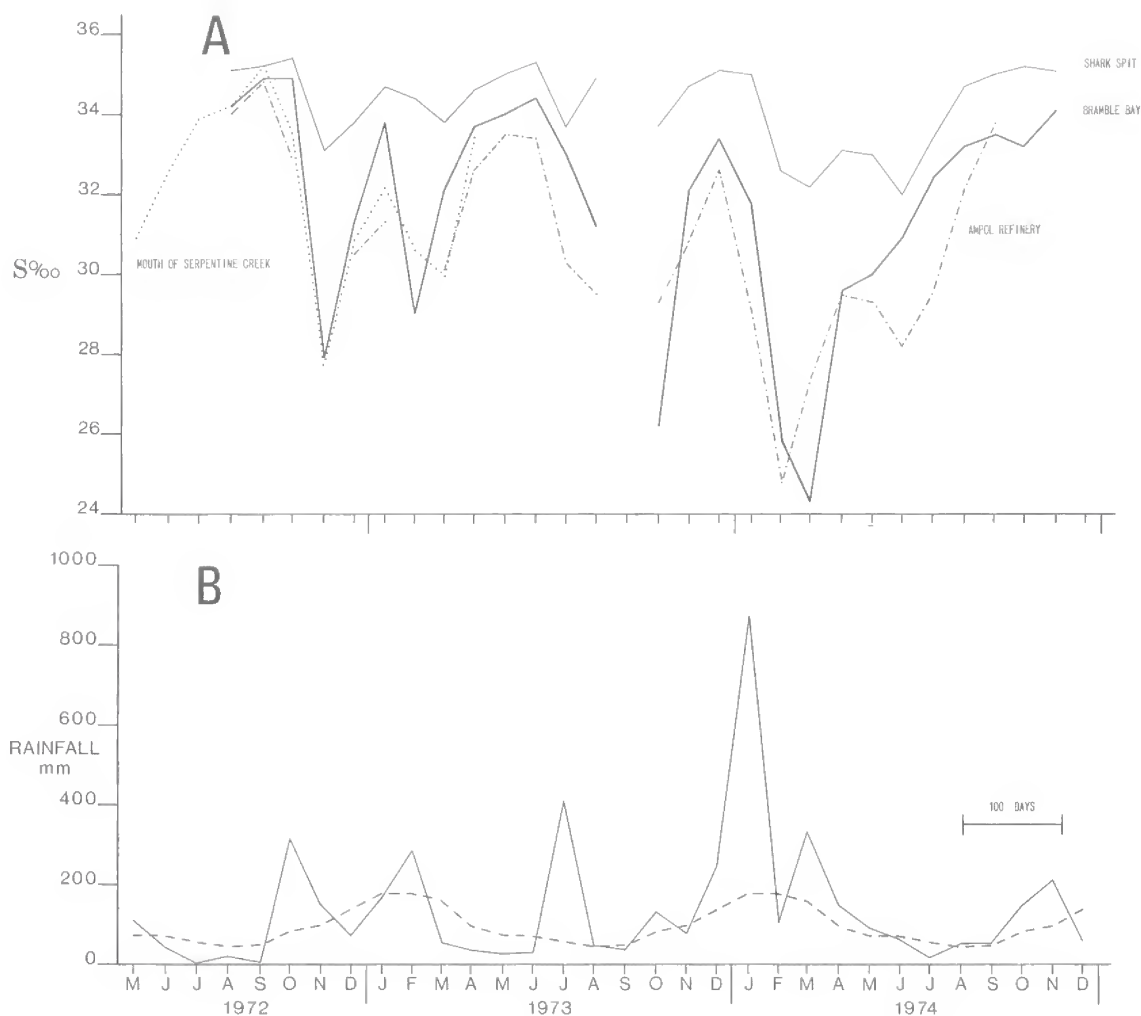


FIG. 3A: Salinities over the period Mar. 1972 to Dec. 1974, monthly means plotted at Middle of each month. Original data from CSIRO Division of Fisheries and Oceanography at localities mentioned.

FIG. 3B: Rainfall data from catchment of Brisbane R. (see text). Monthly values from Mar. 1972 to Dec. 1974 (continuous line) compared with monthly averages over years 1915–1972 (dotted line).

(about $2^{\circ}/\text{‰}$ below Shark Spit) and an annual range of *c.* $28^{\circ}/\text{‰}$ to $35^{\circ}/\text{‰}$. These assumptions are supported by the monthly means from the shorter hydrographic study near our site 6 (Fig. 3A, dotted line). In the flood year the average would be *c.* $30^{\circ}/\text{‰}$, (about $3.5^{\circ}/\text{‰}$ below that of Shark Spit) with a range from *c.* $24^{\circ}/\text{‰}$ to $34^{\circ}/\text{‰}$, and with approximately twice the variance of the pre-flood year.

In both years, salinity variability measured as variance was, somewhat surprisingly, greatest at the Bramble Bay station, followed by the mouth of the Brisbane R., 6 m, 11 m, and Shark Spit in that order.

Fig. 3A shows four occasions of salinity reduction, with three in the pre-flood period (Nov. 1972, Feb. 1973 and July 1973 possibly until Oct. 1973). In Jan. 1974 even before the flood, salinities were reduced in Bramble Bay and near the mouth of the Brisbane R. The greatest reduction at the mouth of the Brisbane R. was in February 1974 but at Bramble Bay and at Shark Spit was in Mar. 1974. High salinities returned about Aug. 1974. A further reduction occurred at Shark Spit and the mouth of the Brisbane R. (but not at Bramble Bay) in June 1974, and this is attributed to the rainfall accompanying the cyclone of Mar. 1974.

It is clear that the flood of Jan. 1974 followed by the Mar. cyclone produced severe, widespread and

prolonged reductions in salinities in Bramble Bay and elsewhere in Moreton Bay.

RAINFALL: In a recent study of the pre-flood benthos of Serpentine Ck., Stephenson and Campbell (1976) showed a close inverse relationship between salinity at the mouth of the Creek and rainfall at the Brisbane Weather Station. In the present case, with a main interest in the flood, rainfall from a much wider area is considered, and a variable time-lag between rainfall and reduction of salinities is to be expected.

Following Raphael (1974) rainfall data were obtained for four weather stations considered representative of the catchment of the Brisbane R. These were: Maleny, one of the higher rainfall areas in the region of the Stanley R.; Kalbar, in the region of the Bremer R.; Crow's Nest, in the region of Lockyer Ck; and Brisbane City. Values for these stations were averaged on a monthly basis covering the period of direct interest, and mean values for the years 1915 to 1972 were also obtained. These data are given in Fig. 3B.

Between Mar. 1972 and Nov. 1973 there were three periods in which rainfall was distinctly above average: (i) Oct. 1972, (ii) Feb. 1973, and (iii) more markedly, July 1973. These correspond to salinity reductions with about a month's delay in (i) and (ii), and with a more prolonged effect in (iii).

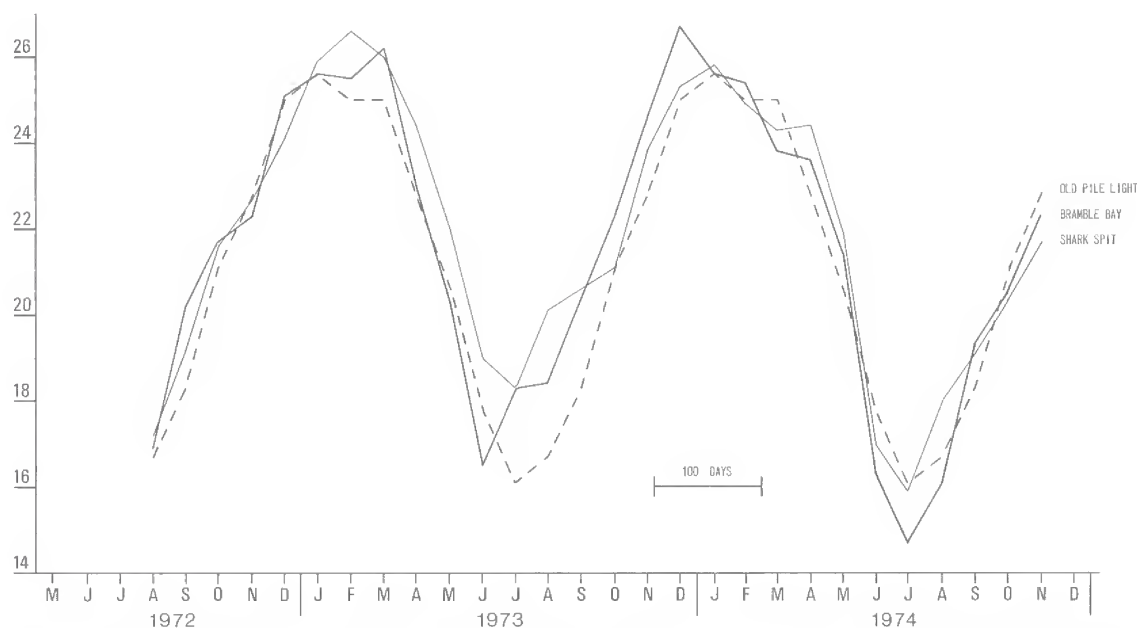


FIG. 4: Water temperatures in $^{\circ}\text{C}$, data plotted at middle of each month. Continuous lines, CSIRO hydrographic stations, Apr. 1972 to Nov. 1974. Dashed line—Ole Pile Light monthly averages over years 1931–1950.

TABLE 2: TEMPERATURE IN °C AT FOUR HYDROGRAPHIC STATIONS; MONTHLY SAMPLES OVER TWO YEARS

Station	Preflood year (Aug. 72–July 73)			Postflood year (Oct. 73–Sept. 74)		
	mean	range	variance	mean	range	variance
Bramble Bay ca 5 m	21.66	16.2–25.5	11.06	21.41	14.6–27.0	13.80
Nr. Ampol Refinery ca 6 m	21.54*	16.3–27.0*	14.23*	21.85	14.8–27.4	18.88
Nr. Ampol Refinery ca 11 m	21.49	16.3–25.8	13.80	21.73	14.8–26.7	18.13
Shark Spit ca 29 m	22.25	17.2–26.6	10.55	21.79	15.9–25.8	12.25

*Values for Nov. 1972, Feb. 1973 not available.

Rainfall increased from Dec. 1973 to an exceptionally high value (873 mm) in Jan. 1974, and after a normally wet Feb. (105 mm) again became higher than normal in Mar. (334 mm). The Dec.–Jan. rains produced minimal salinities in Mar. (except at the mouth of the Brisbane R.) while the Mar. rains produced a second salinity reduction in June 1974 (except at Bramble Bay). As stated earlier the combined effects of the two wet periods had not disappeared until Aug. 1974.

TEMPERATURES: Relevant temperature data, obtained by the CSIRO Division of Fisheries and Oceanography are plotted in Fig. 4, with summarising data in Table 2. Although there is greater variability in the flood year there are no obvious or immediate relationships to the flood.

SEDIMENTS: Maxwell (1970) investigated the sediments of Moreton Bay and showed in Bramble Bay there was an inshore area of medium sand (modal type) and an offshore area of fine sand. Raphael (1974) noted that sediments were muddier than Maxwell's results indicated, and undertook sediment collection and analyses. The results showed considerable and apparent random variation and Stephenson, Raphael and Cook (1976) were only able to derive meaningful topographical patterns by considering the finest and coarsest sediment fractions.

Grab samples made in Mar. 1974, (one month after the flood) showed that a layer of soft oozy mud had settled over the entire sampling area. The layer ranged in thickness from 1–5 cm without any obvious topographical pattern in thickness. It was suggested earlier that sediments scoured from the Brisbane R. had settled in the eastern part of the sampled area and reduced depths, and the widespread layer of soft mud had clearly originated in the same way, no doubt as the last sediment fraction to settle. Recently dead bivalves were buried beneath the mud. Four months after the flood, the fine soft layer was doubtfully recognisable. It was suspected that some had been dispersed by water movements and some had consolidated.

In the hopes of quantifying the sediment settlement, and showing that the grounds had become 'permanently' more muddy, sediment samples were collected at the end of the period of biotic sampling—in Mar. 1975. Meanwhile the heterogeneity in the preflood sediment data had become apparent, and this was attributed to hand selection of aliquots from within 0.1 m² van Veen samples. At this stage the preflood data were regarded as unreliable and the collecting methods were revised, however further analyses showed that the preflood data were of value.

Raphael's (1974) data on the present 27 sites were considered, involving triplicate analyses (at 6 month intervals); we neglected her additional data on 21 further sites (involving duplicate annual analyses). Time changes in the data, obtained in June 1972, Dec. 1972, and June 1973 are not apparent, and only area patterns were sought.

Sites were classified using as attributes the mean of the percentages of sediment grades in the three samples. As a preliminary the variability in the data was assessed as the average probable error in the means of the mud percentages of the three samples; this was *c.* 2.75% in an average of *c.* 50%. It is felt that only a negligible fraction of this would be due to seasonal variation. The data we quote are given to the nearest 1%, but are clearly less accurate than this except in the rarer fractions.

Raphael's analyses and the present ones, were by wet sieving with sieve sizes (in mm): 2.00, 1.00, 0.50, 0.25, 0.125, and 0.063. The grades retained are referred to as gravel (=shell), very coarse sand, coarse sand, medium sand, fine sand, and very fine sand respectively. The fraction passing the finest sieve is referred to as mud.

In classification the Bray-Curtis dissimilarity measure and group-average sorting were used—see Clifford and Stephenson (1975) for explanation of these terms.

The dendrogram of the preflood sediment site-groups is given in Fig. 5 and originally the seven groups marked X on this figure were chosen. Three groups are small, comprising sites 16, 17+23, and

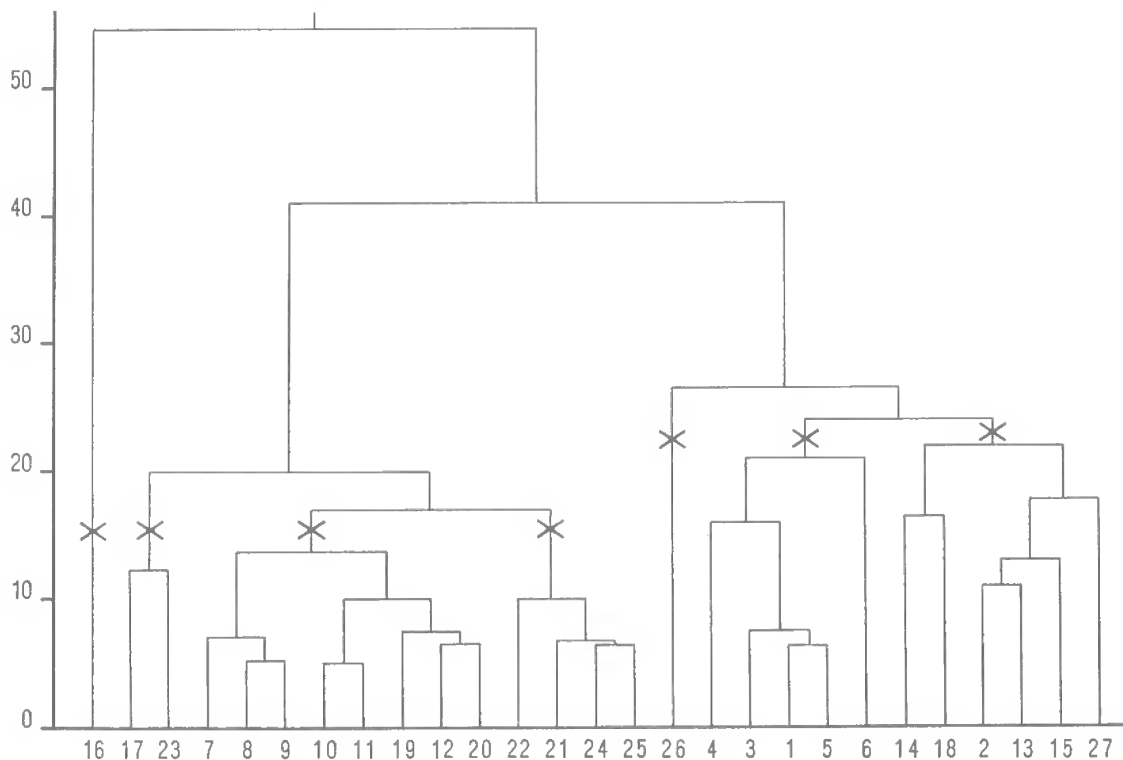


FIG. 5: Dendrogram of sites classification using pre-flood sediments. Vertical scale percentage 'Bray-Curtis' dissimilarity, X indicates site-groups originally accepted.

26, and of these the second and third were readily reallocated. Mean percentages of sediment fractions in the five resultant site-groups are shown in Table 3A and the site-groups are map plotted on Fig. 6.

Fig. 6 shows that a topographically coherent pattern is obtained and in conjunction with Table 3A the overall situation is:

Group 1, site 16, low mud percentage, and high percentages of coarse grades.

Group 2, sites 2, 13, 14, 15, 18, 26, 27,—inshore and mostly adjacent to the Brisbane R., with an isolate (site 2) off the mouth of Cabbage Tree Ck, broad spectrum of sediment fractions.

Group 3, sites 1, 3, 4, 5, 6,—most inshore sites, sediments mostly mud and very fine sand.

Group 4, sites 7, 8, 9, 10, 11, 12, 17, 19, 20, 23,—the bulk of the sampled area and at intermediate depths, sediments predominantly (c. 2/3) mud.

Group 5, sites 21, 22, 24, 25,—the deepest and most offshore sites, sediments very predominantly (c. 4/5) mud.

Overall, the western part of the sampled area gives groups with increasing muddiness in deeper water. The eastern part has less muddy sediments, and presumably is under influence from the Brisbane R. The coarse sediments at site 16 probably have a biotic origin (dead shell material).

In the postflood sediment sampling, we used a Smith McIntyre grab covering half the surface of a normal 0.1 m² grab, but penetrating to the same depth, and took entire grab samples back to base. Here they were homogenised by vigorous stirring in a larger container, adding water if necessary. After settling and if necessary partially evaporating in air, three subsamples were taken simultaneously with separate 5 cm corers and each closed at base by a hand-manipulated metal disc. Sediment analyses were carried out separately on each core, and the means of the three determinations were used. The average probable error of the means of the most variable fraction, the mud, was now c. 0.4% in values averaging 58%, and the results are hence about 7 times more accurate than the pre-flood data.

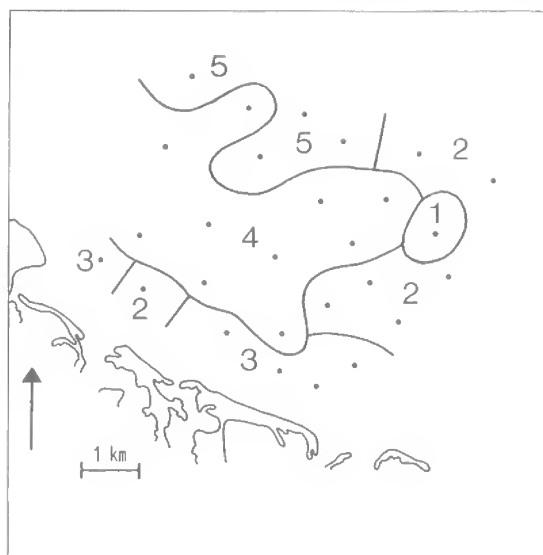


FIG. 6: Topography of site-groups from preflood sediments.

Data were processed as before and the dendrogram of the sediment site classification is given in Fig. 7. Initially we accepted the seven site-groups marked X on that figure, and then reallocated the group consisting of a single site (12). The six resultant groups are map plotted on Fig. 8. Average percentages of each grade of sediment in each site group are given in Table 3B.

Comparison of preflood and postflood sediments on a gross basis indicates an average increase in the mud percentage from 51% to 58%. It was suspected that, in the postflood sampling, the snapping of the jaws of the Smith McIntyre grab caused the loss of some softer material on the surface of the samples. If so the difference in mud percentages between postflood and preflood samplings would have appeared greater.

Comparison of Figs. 6 and 8 shows considerable changes, with the western side of the sampled area the least changed and with inshore (group 3), middle (group 5) and offshore (group 6) groups still apparent. However the mud percentages of the inshore and middle groups have increased by c. 10%, while the offshore group (with a mud percentage unchanged at c. 82%) has moved its boundary inshore. The eastern side of the sampled area is markedly changed into a mosaic pattern. The area with coarsest sediments (group 1) now includes site 27 as well as site 16, suggesting a scouring effect. The next coarsest (group 2) has the same broad spectrum of sediment fractions as in the preflood group 2 and appears relatively unaltered by the flood.

BIOTIC DATA

GENERAL CONSIDERATIONS

Methods of collection of biotic data are as described in the preflood paper (Stephenson,

TABLE 3: MEAN PERCENTAGES OF SEDIMENT FRACTIONS PER SITE IN THE SEDIMENT SITE-GROUPS. A—PREFLOOD, B—POSTFLOOD

Sed. site-grp.	Sites in Site-group	Mean percentages of sediment fractions						
		V.F. Mud	F sand	M sand	C sand	V.C. sand	Gravel (= shell)	
A								
1	16	5	2	13	23	24	9	25
2	2, 13-15, 18, 26, 27	30	15	16	20	6	2	12
3	1, 3-6	39	31	16	6	1	1	7
4	7-12, 17							
	19, 20, 23	66	10	4	5	3	1	10
5	21, 22, 24, 25	81	6	3	3	1	1	6
B								
1	16, 27	13	3	11	30	24	5	15
2	13, 14, 18	25	22	29	14	5	1	3
3	1-6, 15, 17	50	29	9	5	2	1	5
4	12, 19, 24, 25	70	9	8	5	4	1	3
5	7, 8, 9, 11	77	12	3	1	1	1	6
6	10, 20-23, 26	83	6	4	1	1	1	4

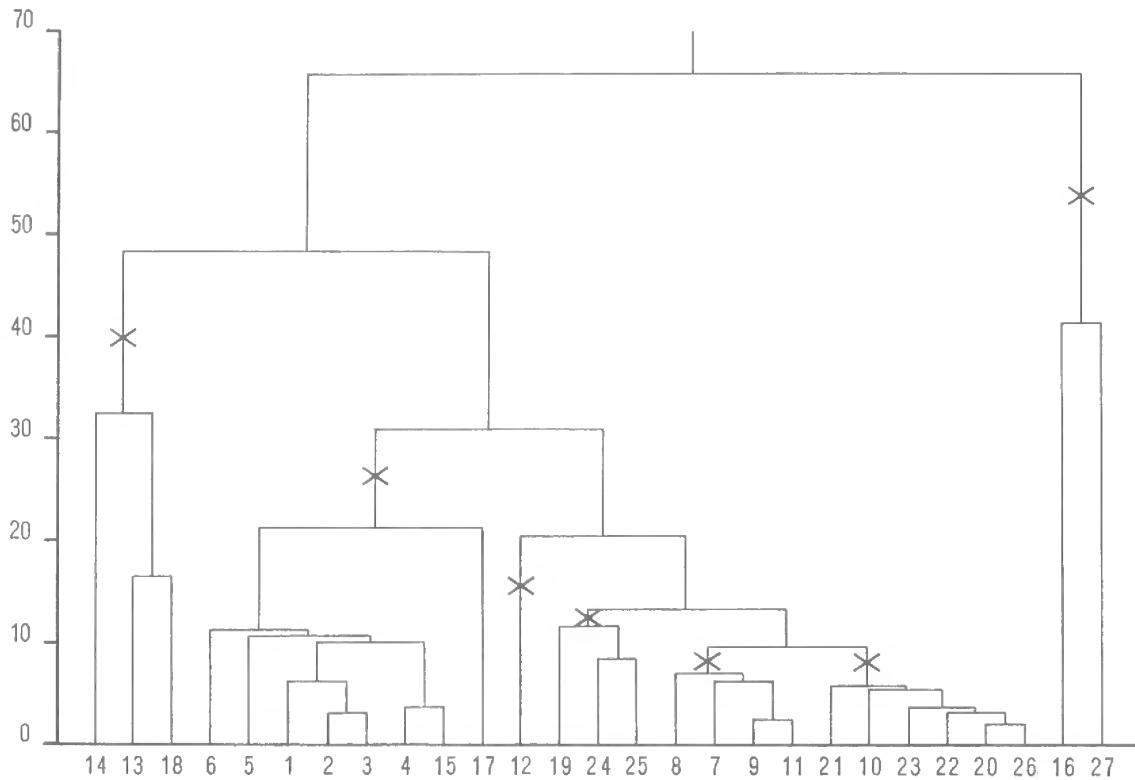


FIG. 7: Dendrogram of sites classification using postflood sediments. Vertical scale percentage 'Bray-Curtis' dissimilarity, X indicates site-groups originally accepted.

Raphael and Cook 1976). Species identifications were almost exclusively by comparison with the earlier reference collections. Individuals of each species in each sample were counted and recorded.

Analyses of data were similar to those of the earlier paper, but included different derivatives of the data.

The original data comprise a 3D matrix of 182 species (s) \times 27 sites (q for quadrats) \times 12 times (t) containing meristic values (whole numbers). We declare a main interest in the times dimension of the matrix, with this divisible into *preflood* comprising t_1 to t_7 (June 1972 to Dec. 1973) and *postflood* comprising t_8 to t_{12} (Mar. 1974 to Mar. 1975). One set of derived data are in binary form (i.e. recording the presence or not recording the presence of species), but otherwise the matrix is identical with the original.

The easiest way to handle either of the 3D matrices is to summate (and then possibly to average) across a specified axis. The various summations are considered later.

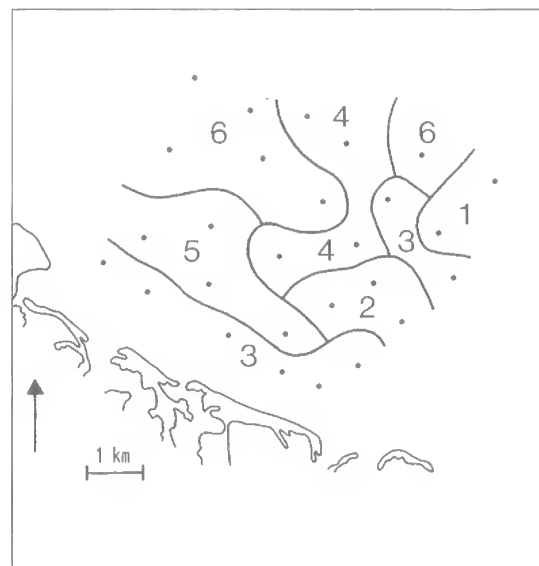


FIG. 8: Topography of site-groups from postflood sediments.

EFFECT OF THE FLOOD ON ALL SPECIES IN ALL SITES

To investigate this we first summated across the species axis in the two previous matrices and derived two $t \times q$ matrices with dimensions 12×27 in each case. The values in the meristic matrix are the sample populations of all species, which are the numerical equivalent of biomass which we designate n , while the values in the summated binary matrix are the number of species in each sample which we designate s . The latter are the species densities per sample (Hurlbert, 1971) and are a simple measure of diversity. A great number of other diversity (and evenness and equitability) measures are also available, and we used the standardised Shannon diversity to base 10 which we designate d . It is the diversity per individual in a given sample. As a result we have three 2D matrices of $t \times q$, containing values of n , s , and d respectively.

We are more interested in t than q , and particularly in how sample parameters change after the flood. This is most easily approached by a further summation and averaging over sites. The matrices are each now collapsed into a one-dimensional array. The n values give a mean n or \bar{n} array, these being the population per sample at a given time averaged over all sites. The s matrix gives an \bar{s} array, values being species densities per sample at a given time, again averaged over sites. Similarly from d we get \bar{d} values. Because occasional very high values of n bias \bar{n} we also used mean $\log(n+1)$ data which approximate to geometric means of n .

Values of the above (see Table 4) suggest that, with all four sample parameters, there are immediate decreases after the flood (in $t8$, Mar. 1974). To show significant differences necessitates parametric tests and these require that the data be 'at random', and have normal distributions or can be transformed to normality. These constraints apply only to the preflood data and previous analyses data have shown negligible seasonal trends (Stephenson, Raphael and Cook 1976) so they can be taken as approximating to random samples.

TABLE 5: MOMENT COEFFICIENTS OF SKEWNESS (γ_1) AND OF KURTOSIS (γ_2) OF DIFFERENT FORMS OF MEANS DATA AFTER VARIOUS TRANSFORMATIONS, (DATA FROM TABLE 4)

Mean data on sites	Transformation	γ_1	γ_2
s	none	0.17	1.68
	square root	0.09	1.59
	\log_{10}^*	0.02	1.52
n	\log_{10}	0.16	2.67
Mean $\log(n+1)$	none	-0.31	1.94
	squaring	-0.21	1.81
	antilog minus 1*	0.02	1.55
d	none	-0.74	2.34
	squaring	-0.63	2.20
	antilog	-0.59	2.12
	5th power	-0.38	1.88
	10th power*	0.01	1.65

*Optimal transformations (γ_1 and γ_2 nearest to zero).

Various transformations were applied to the rows of preflood data and normality was judged by the moment coefficient of skewness (γ_1) approximating to zero (see Table 5).

For s values a log transformation is acceptable and for n values detransformation of mean $\log(n+1)$ values is acceptable. The d values are negatively skewed and require the 'ridiculous' 10th power transformation to remove this skewness. In Table 5 moment coefficients of kurtosis (γ_2) are also tabulated, and it will be noted that transformations removing skewness leave considerable positive kurtosis. Using the above transformations, and accepting that data are still not normal, we felt justified in using parametric tests. The test selected, the F test, is identical with the t test as applied below.

The seven preflood values were compared with a single postflood value viz. $t8$, $t10$, $t11$, and $t12$ respectively, and results are given in Table 6.

Based on Tables 4 and 6 we can tentatively group the five postflood times into (a) early postflood with

TABLE 4: MEAN NUMBER OF SPECIES PER SITE (s), MEAN NUMBER OF INDIVIDUALS PER SITE (n), MEAN $\log_{10}(n+1)$ VALUES AND MEAN INDIVIDUAL SHANNON DIVERSITY (d) IN THE DIFFERENT TIMES

	Preflood Times							Postflood Times				
	1	2	3	4	5	6	7	8	9	10	11	12
s	13.56	13.74	15.89	9.41	10.22	12.74	9.81	2.26	4.15	7.30	6.96	6.48
n	130.1	102.0	107.3	53.0	199.1	367.6	150.2	22.2	90.6	303.7	292.0	412.55
mean $\log_{10}(n+1)$	1.87	1.67	1.86	1.65	1.48	1.82	1.64	0.74	1.02	2.06	2.11	2.21
d	0.69	0.77	0.80	0.63	0.80	0.76	0.73	0.24	0.38	0.36	0.25	0.23

TABLE 6: RESULTS OF SIGNIFICANT TESTS OF PREFLOOD VALUES COMPARED WITH SINGLE POSTFLOOD VALUES INDICATED BELOW. DATA TRANSFORMED FROM TABLE 1

	t8	t9	t10	t11	t12
\bar{s}	lower**	lower**	lower	lower*	lower*
mean log ($n + 1$)	lower*	lower	higher*	higher*	higher*
\bar{d}	lower	lower	lower	lower	lower

** indicates 0.01 significance or better, * indicates 0.05 significance, no star indicates difference not significant.

devastation and early recovery—times 8 and 9; (b) intermediate—time 10. By two measures recovery is still proceeding (mean log ($n + 1$) and s), by the third d it is at or past the postflood peak; (c) late postflood—times 11 and 12. It is of interest to note that diversities immediately after the flood are identical with those in the later period. However the values of s and n are quite different in the two; to this extent the d values conceal useful information.

EFFECTS OF THE FLOODS UPON ALL SPECIES IN SEPARATE SITES

The above analyses have shown effects averaged over all sites, and involve taking the entire sampled area and the entire biota as the unit of measure. In the present analyses we treat the sites separately. We again consider the $t \times g$ matrices involving summation over species, but omit the final averaging over sites. Only two such matrices were considered involving s values (species densities per sample) and n values (populations per sample).

For each site the seven preflood values of a sample parameter were compared in the first instance with each postflood value taken singly. As before the F test was used following an appropriate transformation of the preflood data.

In some cases where a 7:1 comparison failed to show a significant difference it was suspected that a 7:2 or 7:3 comparison, involving additional postflood values, would show the effect. However the

basis of the F test is now further eroded; while the preflood samples can still be regarded as being at random there are trends and not randomness in the postflood period. We decided to retain the parametric testing but to interpret results with caution.

Another reason for caution is that prior to the analyses, (and unfortunately) species reduction had been effected (see later). Only 74 species are used in the present analyses and this will particularly effect s , although n will be negligibly affected.

Effects of transformations upon normality of preflood values were essayed by computation of moment coefficients of skewness (γ_1) as before. It appeared that, for a given form of data, there was a different optimal transformation for each site and this is yet a further reason for caution in interpretation. The mean coefficient of skewness over all 27 sites was used, and the transformation which reduced this closest to zero was accepted. For the s data \sqrt{s} was used (mean $\gamma_1 + 0.10$) and for n data log ($n + 1$) (mean $\gamma_1 + 0.36$).

Tabulating the numbers of sites with 'significant' changes in (s) and in (n) (see Table 7) shows that s and n data give comparable results, with effects apparently least in roughly the middle of the postflood periods of sampling. The high numbers of affected sites will be noted.

Considering the data on a site by site basis, and considering each postflood time separately revealed that all sites showed 'significant' changes in

TABLE 7: NUMBER OF SITES WITH SIGNIFICANT CHANGES IN NUMBERS OF SPECIES PRESENT (s) AND IN TOTAL POPULATIONS OF ALL SPECIES (n) POSTFLOOD TIMES (BELOW) COMPARED WITH PREFLOOD TIMES

	t8	t9	t10	t11	t12	t8 + 9	t9 + 10	t8 + 9 + 10	t11 + 12	Summation over all comparisons
s	20	14	4	4	8	22	15	21	9	25
n	19	16	10	10	13	23	6	11	14	26

either *s* or *n* values on one or another occasion. Four sites showed no 'significant' changes in *s* viz. sites 8, 9, 10, 11 and two no 'significant' changes in *n* viz. 1, 14. Cases of 'significant' changes are given in Table 8A and B, with sites arranged in groups.

Comparison of Table 8A (*s*) and 8B (*n*) shows that the populations data (*n*) show much more change than species numbers (*s*), mainly due to 'significant' increases in populations of sites from time 10 onwards—there were no 'significant' increases in numbers of species in any of the sites at any time; and that the groupings of sites show scant resemblance between the two sets of data, the only obvious resemblances being that transient decreases form the largest group in both cases and contain some sites in common (3, 12, 20 and 27).

Two topographical patterns are revealed by these data. Sites with very transient increases in the number of species (*s*) are generally distant from the

TABLE 8: SITES SHOWING 'SIGNIFICANT' CHANGES IN NUMBER OF SPECIES (A) OF INDIVIDUALS OF ALL SPECIES (B) WHEN SINGLE POSTFLOOD SAMPLINGS (AS LISTED) ARE COMPARED WITH PREFLOOD SAMPLINGS (TIMES 1-7)

A. NUMBERS OF SPECIES (ALL DECREASES)

Designation of sites	Site nos.	t8	t9	t10	t11	t12
Very transient decrease	4	*				
	21	*				
	22	*				
	23	*				
Transient decrease	1	*	*			
	3	**	*			
	6	**	**	*	*	
	7	*	*			
	12	**	*	*		
	13	*	**			
	20	*	**			
	26	*	*			
	27	**	*			
Delayed onset decrease	2		**			
	14					**
	25					*
Permanent decrease	18	**	**		**	**
	19	**	**	*	*	**
Decreases of uncertain pattern	5	**				*
	15	**		*		
	16	**	**			**
	17	**				*
	24	**	**			*

B. NUMBER OF INDIVIDUALS (DECREASES AND INCREASES)

Designation of sites	Site nos.	t8	t9	t10	t11	t12
Very transient decrease	5	*				
	17	**				
	21	*				
	22	**				
	23	**				
Transient decrease	2	**	**			
	3	**	**			
	4	**	**			
	11	*	**			
	12	**	*			
	15	*	**			
	20	*	**			
	25	*	*			
	27	**	*			
Delayed onset decrease	6		*			
	8				*	
	9		*			
	19		**			
	26		*			
Permanent decrease	7	**	**	**		**
	13	**	*	**	**	*
Decreases of uncertain pattern	16					*
	18	**	**		**	
	24	**		*		
Transient increase	11				**	
	16	*				
Delayed onset increase	19					*
	21					**
Permanent increase	10			**	**	**
	15			**	**	**
	17			**	**	**
	20			*	*	*
	22				**	**
	26			**	**	**
Increases of uncertain pattern	12			**		**
	27			**		*

*0.05 probability

**0.01 probability

Brisbane R. Sites with increases in population at one time or another form a band at intermediate depths (see Fig. 9).



FIG. 9: Sites with increased populations (at one time or another) after the flood—vertical lines, and with very transient decreases in numbers of species—horizontal lines.

EFFECTS OF THE FLOODS UPON SPECIES

Here we consider species for the first time, and operate with $t \times s$ matrices, derived from the 3D matrices by summation across sites.

Data were reduced by elimination of the rarer species—those with <12 individuals in the pre-flood sampling of the wider area of original study (27 + 21 sites). This insured that species were numbered as in Stephenson, Raphael and Cook (1976). The choice of cut-off level followed preliminary analyses which showed that rarer species never gave noticeable differences between pre-flood and postflood data. The 74 species retained for these analyses are listed in the Appendix together with their code numbers. Subsequently species are generally referred to by code number, when names

are cited generic names are used except when more than one species of a genus was considered.

Two $t \times s$ matrices were considered. By summation of meristic data we obtain the total population in all sites of a species at a given time and this we designate p (for population). Similar summation of binary data gives the number of sites (out of 27) occupied by a species at a given time and this we designate q (for quadrats). It measures the ubiquity of a species in space at a given time.

To determine whether a species shows changes in population or ubiquity by the first period after the flood we compare seven preflood values with the first postflood value. Additional 7:1 comparisons were made using later postflood times, and further comparisons with 7:2 and 7:3 arrays. Transformations were applied to the preflood values (only) and as before to reduce skewness to minimal values, different transformations were required in each case; following Taylor (1961, 1971) this is entirely expected. For present purposes we worked with 12 hopefully representative species and chose the transformations which gave the mean of the moment coefficients of skewness closest to zero. For q values this involved no transformation (mean $\zeta_1 + 0.07$) and for p values the $\log(p + 1)$ transformation (mean $\zeta_1 + 0.18$). The F test was used with the transformed data.

The numbers of species showing 'significant' changes in ubiquity and in populations in the different postflood times were roughly comparable (see Table 9). Effects are least near the middle of the postflood observations because early decreases and later increases are balancing.

Data were next considered on a species by species basis. Using data from each postflood time separately showed that 36 of the 74 species did not show any 'significant' differences. These species were: 2, 4, 8, 23, 24, 30, 31, 32, 35, 37, 38, 40, 42, 43, 46, 47, 48, 49, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 63, 65, 66, 67, 69, 70, 71 and 74. Twenty-six of these are from the 37 species in the lower half of the abundance hierarchy and here the preflood values are generally too low and too variable for 'significance' to show. However apart from three cases

TABLE 9: NUMBER OF SPECIES WITH 'SIGNIFICANT' CHANGES IN NUMBER OF SITES OCCUPIED (q) AND IN TOTAL POPULATIONS IN POSTFLOOD TIMES (p) COMPARED WITH PREFLOOD TIMES 1-7

	t8	t9	t10	t11	t12	t8 + 9	t9 + 10	t8 + 9 + 10	t11 + 12	All comparisons
q	10	6	7	11	16	14	13	17	16	27
p	16	11	6	9	11	27	19	22	19	34

(spp. 32, 40, 46) the mean preflood recordings were at least four times those of times 8+9.

Sixteen of the remaining species showed 'significant' differences only when a pair of postflood values was compared with the preflood data: in each case the postflood values were the lower. The species were 7, 21, 22, 25, 26, 28, 29, 33, 36, 41, 44, 50, 61, 68, 72 and 73.

The remaining species showed 'significant' effects by one measure or another. They form two (overlapping) groups, the first showing decreases

(17 spp.) and the second showing eventual increases (7 spp.). These groups with further groupings within them, are given in Table 10.

Table 10 shows that five species show a very transient decrease (only 'significant' in time 8) viz. spp. 12, 13, 20, 27 and 39, while two more show a transient decrease viz. spp. 5 and 19. Two show a delayed onset of decrease (spp. 16 and 64) but one of these is a weak case (sp. 16). The largest group is of seven species showing a permanent decrease viz. spp. 2, 6, 10, 14, 17, 18 and 45.

TABLE 10: SPECIES SHOWING 'SIGNIFICANT' CHANGES IN NUMBER OF SITES OCCUPIED AND/OR IN POPULATION IN ALL SITES WHEN COMPARING SINGLE POSTFLOOD SAMPLINGS (AS LISTED) AND PREFLOOD SAMPLINGS (TIMES 1-7)

Designation of species	Spp. no.	Sites occupied (<i>q</i>)					Populations all sites (<i>p</i>)				
		t8	t9	t10	t11	t12	t8	t9	t10	t11	t12
Very transient decreases ¹	12	*					**				*
	13						*				
	20						*				
	27	*					**	*			
	39	*					*				
Transient decreases ²	5	*	*	*			*	*			
	19	*	*	*	*		*	*	**	**	
Delayed onset decreases ³	16							*			
	64				*	*				**	*
'Permanent' decreases ⁴	2	*	*		*		**	**	**	*	**
	6	**	**	**	**	**	**	*	*	**	*
	10						*	*	*	*	*
	14	**			*		**	*		*	*
	17	*	*	*		*	**	**	**		**
	18						*		*	*	*
	45						*	*			*
Decreases of uncertain pattern ⁵	9	**	**		*	**	**	*			
Transient increases ⁶	11							*			
	12				**						
	15			**							
	34			**	**						
	62				*						
'Permanent' increases ⁷	1			**	**	**					
	13				*	**				*	**

*0.05 probability **0.01 probability

¹significance only or mostly in first postflood period, t8.

²significance in first four postflood periods t8-t11.

³not significant in early postflood period.

⁴significance essentially unchanged throughout the first five post-flood periods.

⁵elements of two of the above.

⁶not significant at the end of sampling.

⁷significant at the end of sampling.

Five species show a transient increase, mostly shown in times 9 and 10 viz. spp. 11, 12, 15, 34 and 62, while two showed a permanent increase (spp. 1 and 13). The majority of cases of increase are in number of sites (i.e. area) occupied rather than in populations and a noteworthy case is the most abundant species of all, sp. 1 *Spisula*. Here populations show no significant change but number of sites occupied changes from a preflood mean of 6.86 to the following values in the last three postflood samplings: 23, 25 and 25 respectively. With only 27 sites available, these are spectacular increases.

EFFECTS ON SPECIES \times SITES AT SELECTED TIMES

ANALYTICAL METHODS: There is a final way of handling a 3D matrix of $s \times q \times t$ and this is to make t separate analyses of $s \times q$. This has been attempted by Hailstone (1972) but encounters problems due first to the considerable computing which is required and secondly because results may be difficult to interpret.

In the present case groupings of times were used. The main chronological discontinuity in the data is between preflood times ($t1-7$) and postflood ($t8-12$). Earlier we have dissected the latter into times 8+9 designated 'early postflood' and times 11+12 designated 'late postflood'. (Time 10 shows intermediate tendencies and was omitted in the present context).

By summation over these periods we derive three 74 species \times 27 sites matrices; actually the postflood sets had fewer species. Each matrix was classified to obtain site-groups characterized by species-groups in the hope of elucidating changes in site-species patterns caused by the flood.

The preflood data have already been classified by Stephenson, Raphael and Cook (1976). For grouping sites we previously used: data transformed by $\log_{10}(n+1)$, Bray-Curtis dissimilarity measure, and group-average sorting. Whereas this technique gave meaningful site-groups in the earlier work (and various other analyses) when applied to postflood data the outcomes verged on the meaningless. As an illustrative example in times 8+9 one site had no species present (site 27) while one (site 20) had one species represented by one individual; these sites are completely dissimilar when using the Bray-Curtis measure. We require a dissimilarity measure in which almost equally impoverished sites show only a small dissimilarity, and the Manhattan metric was chosen. For two sites and recordings of a given species n_1 and n_2 , then for s species the formulation is $\sum_1^s |n_1 - n_2|$. This measure is the numerator of the Bray-Curtis measure, without its standardizing denominator. The method

used for sites in the postflood was then: data transformed by $\log_{10}(n+1)$, Manhattan metric dissimilarity measure, group-average sorting. To ensure comparability it was necessary to reanalyse the preflood data with the same technique.

Site-groups were selected from the dendrograms on two bases: to derive the maximum number of major groups with topographical coherence, and by perusal of the two-way table to ensure that there were the maximum number of conforming species (see later). In each case this resulted in three main site-groups. For the few sites which appeared to have been misclassified reallocations were effected and these increased the topographical coherence of the groups.

For species-groupings we used the Manhattan metric equivalent of the technique used by Stephenson, Raphael and Cook (1976). This involved an extra stage, standardization by total of transformed values prior to obtaining Manhattan dissimilarities. As indicated elsewhere (Stephenson and Campbell 1976) there are several problems concerning species-groupings. If we declare an interest in species as characterizing groups of sites rather than individual sites, species classifications often fail to group together like species.

A species may characterize a site-group in one of two ways. A positive characterization means that the recordings in a given site-group are higher than in the other site-groups, while a negative characterization means that the recordings are lower than in the other site-groups. Of the two, positive characterizations are conceptually more satisfying. Such species can be selected visually, in which case a series of high recordings in the sites of a given site-group 'stand out' from the remainder. There are obvious objections to such a visual method, and an objective technique is desirable. The alternatives are tests based upon the usual tests of significance. Here again objections can be raised. Tests of significance require that the arrays of data which are compared are random samples, and clearly this does not apply in cases like the present in which data have been clustered to optimise dissimilarities. It can be argued that, if after this optimisation, the recordings of a species are not significantly different in the different site-groups, then the data are really at random; this argument we do not pursue. Instead we use the mechanics of a standard test of significance of difference because this closely parallels the results of visual scanning. We avoid the use of the word 'significant' and refer to differences as 'noticeable' or 'outstanding'. The test used is referred to as the 'pseudo-F-test' and was employed using $\log(n+1)$ transformed values. It

identifies species in which variability within site-groups was such as to render differences between means 'non-noticeable', and in the terms of Stephenson, Williams and Cook (1974) it picks out non-conforming species. A level, equating to a probability level of 0.05 in the F test was chosen as cut-off point. It should be noted that the present method involves post-classificatory removal of species.

In the preflood data relatively few species did not conform to the site-groups and the species-groups of the original classification which remained after their removal required only minor re-allocations to give the optimal species-groupings in site-groups. In the two postflood data sets, the species-groupings as illustrated by the dendrograms showed excessive chaining and hence virtually no species-groupings. Most of the species were non-conforming (reflecting the paucity of data) and the small residue of conformers were readily classified by visual inspection of the data.

RESULTS: (i) *Preflood data (summed over times 1-7)*. On the dendrogram of the site-classification (Fig. 10) at just over 20 units of dissimilarity there

are four groups, one containing a single site. This site was reallocated and we accepted the following site-groups:

- A. (inshore): Sites 1-6, 8, 9, 14, 15
- B. (middle): Sites 7, 10-13, 16-20, 26, 27
- C. (offshore): Sites 21-25.

These groupings are map-plotted on Fig. 11 with the equivalent groupings when the Bray-Curtis dissimilarity measure was used shown on Fig. 12. The two plottings are similar in showing inshore, middle and offshore site-groups, with those of the present analyses possibly showing greater correspondence with the distribution of preflood sediments (see Fig. 6).

The dendrogram of the species classification gave nine unequal groups at a dissimilarity level of ca. 1.20. When species not conforming to the site-groups were excluded 47 species remained in three main groups with 6 other species in four other groups. After reallocation of the 6 species, four groups were obtained, the three largest being essentially the original groups. The final groups are given in Table 11, together with the mean number of individuals per site in the site-groups, reduced to the equivalent of a single sampling time.

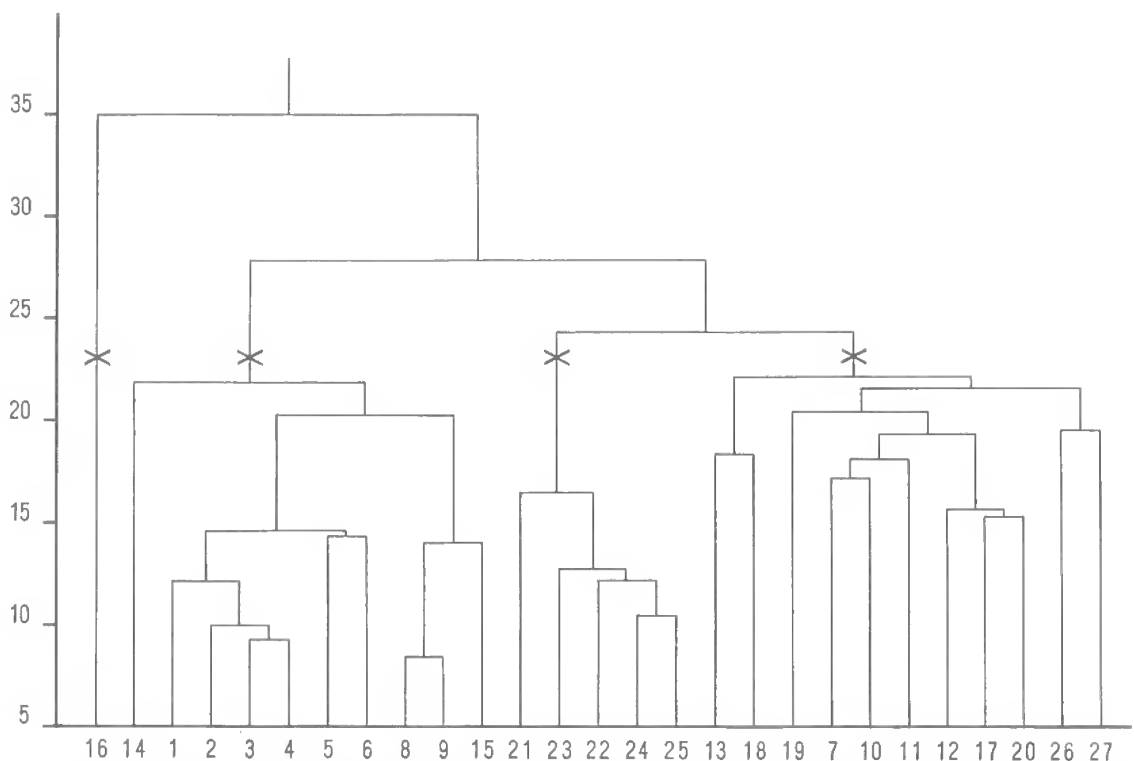


FIG. 10: Dendrogram of sites classification using 74 species, preflood data (times 1-7). Vertical scale Manhattan metric dissimilarity, X indicates site-groups accepted.

TABLE 11: PREFLOOD DATA (TIMES 1-7). MEAN NUMBER OF INDIVIDUALS OF CONFORMING SPECIES PER SITE IN EACH SITE-GROUP, REDUCED TO A SINGLE TIME

Species group	Species no.	Site-groups†		
		A (inshore)	B (intermediate)	C (offshore)
I (inshore spp.)	1	230.2	0.1	0
	3	25.7	5.7	1.1
	9	3.7	0.5	0.3
	11	2.6	0	0
	15	2.2	0.3	0
	16	1.5	0.1	0
	24	0.7	0.3	0.1
	26	1.4	0	0
	40	0.3	0.1	0
	50*	0.2	0.1	0
	54	0.2	0.1	0
	70*	0.2	0	0
II (middle spp.)	5	0.5	5.3	0
	18	0.3	0.9	0
	22	0	0.5	0
	28	0.2	0.4	0
	38*	0	0.2	0
	49	0.1	0.3	0
	59	0	0.2	0
	60	0	0.2	0
	63	0	0.1	0
	68	0	0.1	0
	69*	0	0.2	0
III (offshore spp.)	4	0.3	7.2	39.5
	6	0	0.9	5.5
	7	0	1.5	7.6
	8	0	0.7	1.8
	10	0.9	1.2	2.0
	12	0.6	1.0	2.1
	13	0.1	0.4	4.2
	14	0.5	0.9	1.8
	17	0.4	0.5	0.6
	19	0	0.1	1.1
	20	0.1	0.4	1.5
	21	0.2	0.3	1.3
	23	0.1	0.5	1.1
	25	0.1	0.3	1.0
	29	0	0.2	1.6
	30	0.1	0.4	0.7
	33	0	0.2	0.8
	37	0.1	0.1	0.8
	42	0	0.3	0.5
	45	0	0.1	0.8
	47	0	0.1	0.4
	48	0	0.1	0.5
	53	0	0.1	0.4
	57	0	0	0.5
	58	0.1	0.1	0.4
	62	0	0.1	0.3
	66	0	0	0.3
	72*	0	0	0.3

Species group	Species no.	Site-groups†		
		A (inshore)	B (intermediate)	C (offshore)
IV (avoiding inshore)	41*	0.1	0.3	0.2
	46	0	0.3	0.3

*reallocated species.

†see text.

Referring to Table 11, the 12 species of species-group I positively characterize the inshore sites, and these sites can be given a 'community' name by as many species as are desired: *Spisula* (1), *Xenophthalmus* (3), *Terebellides* (9), *Pupa* (11) etc. The 11 species of species-group II positively characterize the intermediate depth sites which can be described as a 'community' of: *Anadara* (5), tunicate 1 (18), oyster 1 (22) etc. The 28 species of species-group III positively characterize the offshore sites as a *Paratapes* (4), *Amphioplus* sp. (6), *Amphioplus lobatus* (7), *Theora lata* (8), *Amphitrite* (10) etc., 'community'. The two species of group IV viz. *Placamen* (41) and *Trichomya* (46) negatively characterize the inshore sites. It will be noted that, of the three main species-groups, the third group has the most cases of 'overlap' from one site-group to another, and mostly from offshore to middle sites. A few species (10, 12, 14 and 17) also extend appreciably into the inshore site-group.

(ii) *Early postflood (times 8 and 9)*. From the dendrogram of the site classification (Fig. 13) three site-groups were accepted in the present data at a dissimilarity level of ca 4 compared with ca 20 for

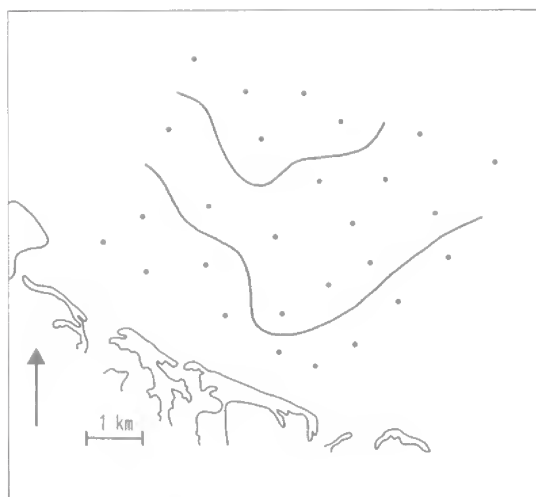


FIG. 11: Inshore, middle and offshore site-groups from preflood biotic data using Manhattan metric dissimilarity.

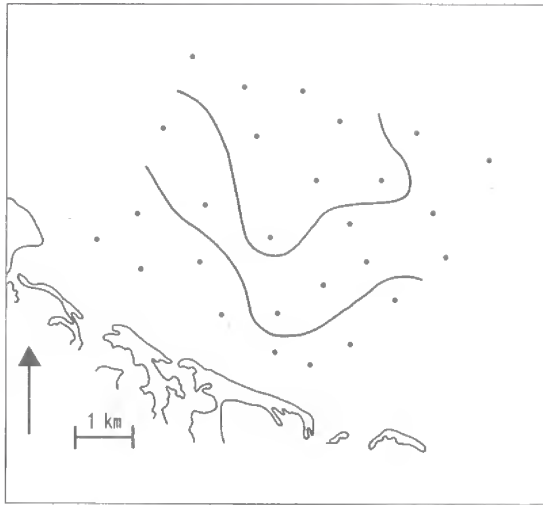


FIG. 12: Inshore, middle and offshore site-groups from preflood biotic data using 'Bray-Curtis' dissimilarity measure.

TABLE 12: EARLY POSTFLOOD DATA (TIMES 8 AND 9). MEAN NUMBER OF INDIVIDUALS OF CONFORMING SPECIES PER SITE IN EACH SITE-GROUP

Species group	Species	Site-groups		
		A (near rivers)	B (offshore)	C (majority)
I (near rivers)	1	321.2	0	0.1
	11	1.3	0	0
	15	1.8	0	0.2
	24	0.4	0	0
II (offshore)	7	0	5.0	0.3
	8	0.1	1.9	0.1
	13	0	8.4	0.5
	14	0	0.5	0.1
	30	0	0.5	0
	33	0	0.8	0
	42	0	0.3	0
	66	0	0.3	0
III (majority of sites)	5	0	0	0.2

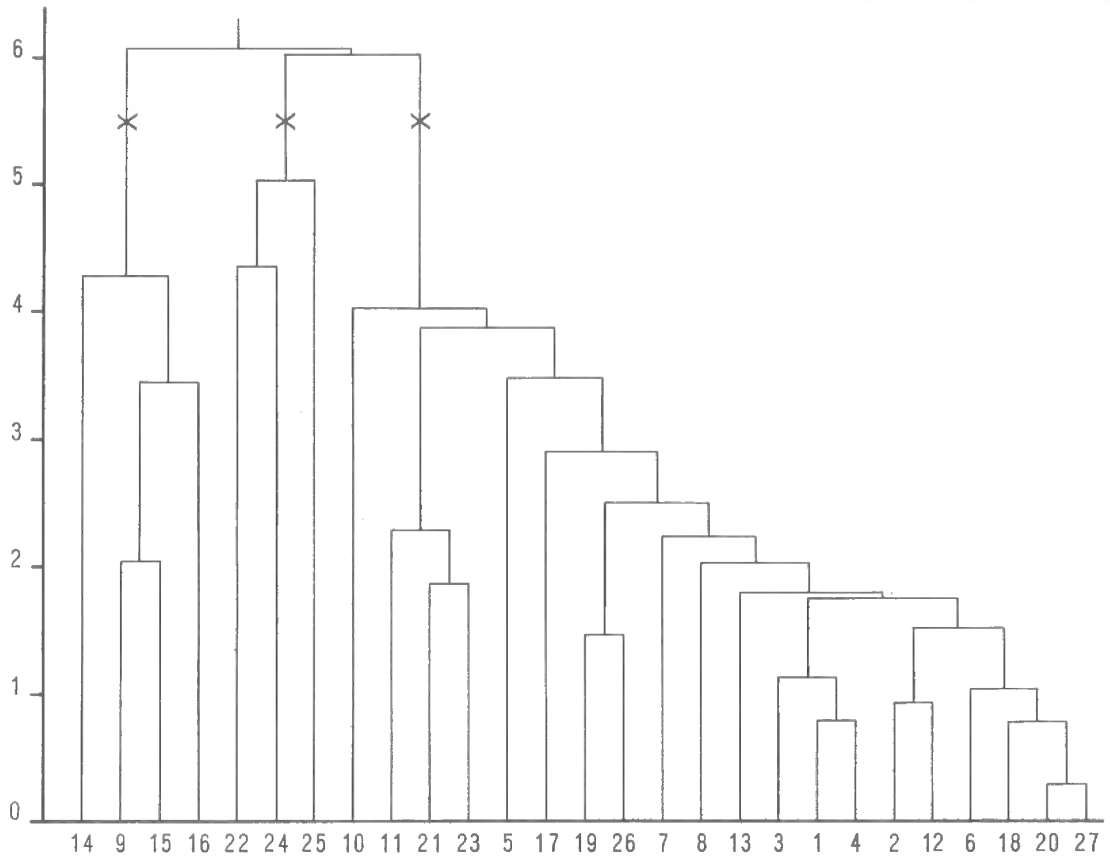


FIG. 13: Dendrogram of sites classification using 74 species, early postflood data (times 8, 9). Vertical scale Manhattan metric dissimilarity, X indicates site-groups accepted.

preflood data. Some of the differences will be due to the reduced sampling intensity (over two times instead of seven) but most of it reflects biotic impoverishment.

The three site-groups are of dissimilar sizes, A comprising sites 9, 14, 15 and 16; next B with 22, 24 and 25; and last C a 'chained' succession of the remainder. Most of site-group A are near the outflows of the Brisbane River or Cabbage Tree Creek, and site-group B are the deepest sites most distant from the Brisbane River. Site-group B corresponds to the offshore site-group of the previous analyses but contains fewer sites.

The species dendrogram showed considerable chaining with only minor groupings and was discarded. Only 13 species conformed to the site-groupings compared with 54 in the preflood situation, and the 13 were grouped visually. Results are given in Table 12 which shows mean recordings per site in a site-group reduced to a single sampling time.

The species form three unequal groups with only one species *Anadara* (5) weakly characterizing the largest site-group (c). Four species characterize the near-rivers site-group which can be described as a *Spisula* (1), *Pupa* (11), *Parcanassa* (15) 'community' in which *Spisula* is markedly dominant. Eight species characterize the offshore sites, which can be described as an *Amphipholis loripes* (13),

Amphioplus lobatus (7), *Theora lata* (8) 'community'.

It is surprising that the near-river site-group (A) which one might have expected to be most affected by the flood, is least affected. The most obvious explanation, that they were recovering at a more rapid rate than the remainder, is supported by the fact that all specimens in sites 14, 15 and 16 at time 8 were extremely small. On this basis sites 9, 14, 15 and 16 are a focus of recolonisation by *Spisula* and possibly the two other species in the group. These are predatory gastropods no doubt feeding on juvenile *Spisula*.

The offshore site-group was previously characterized by 28 species, and now in the immediate postflood samplings is characterized only by eight species. The population of the dominant species *Amphipholis loripes* is higher than before; previously *Paratapes* (4) was the commonest offshore species.

(iii) *Late postflood (times 11 and 12)*. From the sites dendrogram (Fig. 14) three unequal groups were accepted at a dissimilarity level of 8; this compares with the previous one of ca 4 and reflects the fuller data now available for analysis. The two small site-groups, A (sites 24 and 25) and B (sites 20, 21 and 23), are both in the deeper more muddy area most distant from the Brisbane R. The third site-group, C, comprises the 22 remaining sites.

Compared with the early postflood groups the largest group now includes two of the previous groups (majority and near-river) while the previous offshore group has now become enlarged and divided into two groups; collectively these are essentially the same area as the offshore group in the pre-flood data.

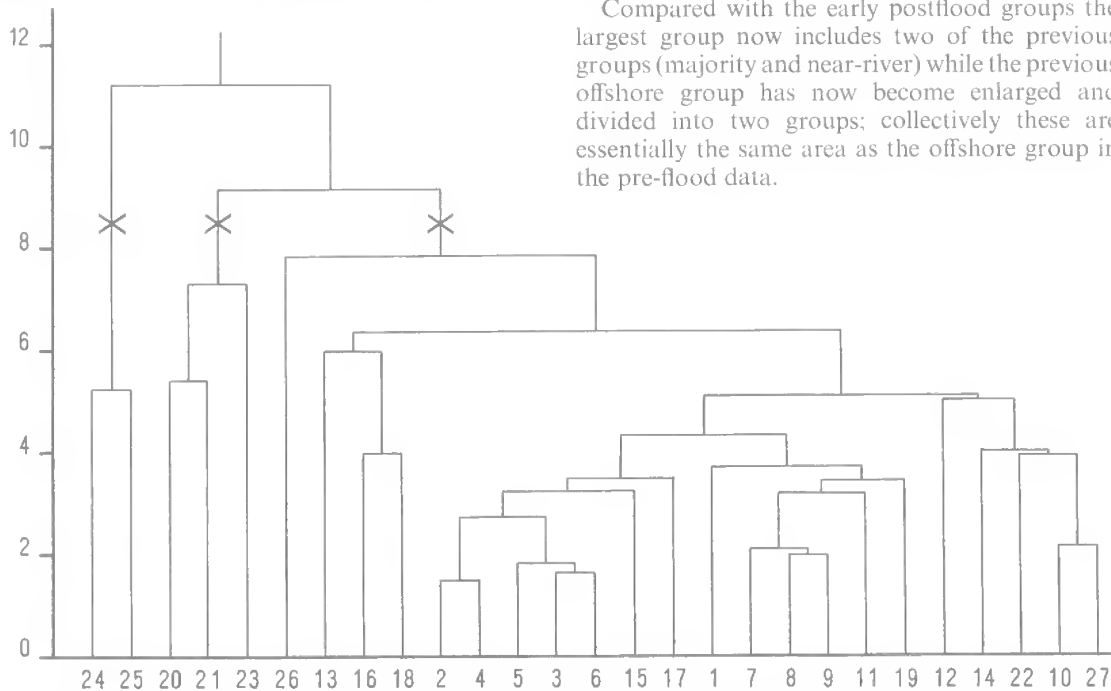


FIG. 14: Dendrogram of sites classification using 74 species, late postflood data (times 11, 12). Vertical scale Manhattan metric dissimilarity, X indicates site-groups accepted.

Only 14 species conformed to the late postflood site-groupings and these species were grouped visually. Results, with mean recordings of species per site per time are given in Table 13. The majority of sites now form a *Spisula* (1), *Parcanassa* (15) 'community'. Clearly the area of dominance of *Spisula* has spread rapidly since the early preflood period, although its population per site is much as before. Both area and population density have increased with *Parcanassa*.

Most of the commoner species which characterized the offshore area in the early preflood again characterize the larger offshore area, but whereas previously eight species were involved there are now twelve. One is less abundant than in early preflood (*Amphipholis loripes* 13) but additional and common species are *Paratapes* (4) and *Amphioplus* sp. (6). Of these the former is now approximately to its preflood density at least within a small area (sites 24, 25).

There are considerable differences between the two offshore site-groups A and B. Site-group B lies within the area of dominance of *Spisula*, and the species is actually commoner here than elsewhere, and also commoner than in its areas of pre-flood dominance. This site-group can be described as a *Spisula* (1), *Paratapes* (4), *Parcanassa* (15), and *Amphioplus* sp. (6) area. Site-group A is without

Spisula and *Parcanassa* and can be described as a *Paratapes* (4), *Amphioplus* sp. (6), and *Theora lata* (8) 'community'.

DISCUSSION

This concerns numerical methodology, the general picture of flood effects, and a possible beginning of a conceptual model of long term changes in the biota of Bramble Bay.

NUMERICAL METHODOLOGY: The only important change from the methods used in the analyses of the biota in the previous paper (Stephenson, Raphael and Cook 1976) has been the use of the Manhattan metric dissimilarity measure instead of the Bray-Curtis. This was because while the Bray-Curtis measure is sensitive to abundance it 'breaks down' in the extreme case of comparing a vacant site with one containing a minimal species recording.

The Manhattan metric extends from zero to an undetermined upper value, and dendrograms must be 'scaled to fit'. (We are grateful to Mr C. Andrews for this routine and for writing all our present programmes).

In the present paper methods of numerical analyses developed for handling biotic data have been applied successfully to sedimentary data. The technique employed the Bray-Curtis measure of dissimilarity (because 'impoverishment' is here not relevant) and classified sites by the group-average method, using percentages of sediment grades as attributes.

EFFECTS OF THE PRESENT FLOODS: All 27 sites were biotically affected one way or another by the flood. Effects on sites were an early reduction in number of individuals present, and throughout reductions in number of species and in (standardized) Shannon diversities. By the end of the study in many sites the populations recovered and then exceeded those of the preflood period. These sites were concentrated in the intermediate sampling depths.

With few exceptions all species which were present in sufficient numbers in the preflood collections to show 'significant' differences were 'significantly' affected. Most of these species declined in areas of occupancy and in overall populations and in most of these cases the declines persisted until the end of the present study i.e. for 14 months.

The main exception was the bivalve *Spisula*. Soon after the flood its area of dominance was changed and restricted but then followed rapid, extensive and dense colonization of the previously depauperate area. By the later postflood periods,

TABLE 13: LATE POSTFLOOD DATE (TIMES 11 AND 12).
MEAN NUMBER OF INDIVIDUALS OF CONFORMING SPECIES
PER SITE IN EACH SITE-GROUP

Species group	Species no.	Site-groups		
		A (Sites 24, 25)	B (Sites 20, 21, 23)	C (remaining sites)
I (not in A)	1	0	387.1	252.5
	15	0	4.3	5.2
II (A only)	30	0.5	0	0
III (B only)	13	0	1.3	0
IV (mostly A, also in B)	4	35.7	12.8	0.3
	6	2.3	2.2	0
	8	1.6	1.4	0.2
	12	0.5	0.3	0
	20	0.8	0.2	0
	33	0.5	0.3	0
V (mostly in B, also in A)	7	2.1	2.8	0
	9	0.2	0.5	0
	14	0.7	1.4	0
	25	0.2	0.9	0

(times 11 and 12) the area of dominance of *Spisula* had extended to cover all but two of the 27 sites and there had been comparable spread of a predatory gastropod *Parcanassa*. Whereas the population per site of *Spisula* in the preflood and late postflood 'communities' was very similar (1150 cf. 1284 per m²), the population of *Parcanassa* more than doubled (11 cf. 26). It is possible that the predator population in the late postflood period was such as to begin reducing the *Spisula* numbers to below their preflood values. It should be noted that other potential predators of *Spisula* are present in low numbers in times 11 and 12.

In a few offshore sites (those most distant from the Brisbane R.) immediately after the flood there remained a small but noticeable remnant of an originally diverse biota with *Paratapes* originally the commonest species. In the later samplings the offshore biota occupied a somewhat larger area and was characterized by more individuals of more species. The area approximated to that of the offshore site-group in the preflood samplings, but the characterizing biota comprised many fewer species.

We now consider changes in environmental conditions during and after the floods, to elucidate possible relationships between biota and abiotic factors. As shown earlier we can neglect for present purposes any abnormalities in water temperatures, and hence concentrate on salinities and sediments. Salinities in that part of Bramble Bay sampled for benthos seem to average about 32.5‰ in a non-flood year. During the preflood year the greatest reduction in salinity from average, due to rainfall, was ca 5‰ and the equivalent value in the flood year was ca 8.5‰. This difference alone would not lead one to expect biotic impoverishment on the scale which was observed.

There is a more impressive difference in the duration of dilution effects during 1974 compared with the previous year. Salinities were already being reduced before the Jan. 1974 floods by rainfall in Dec. 1973 and did not return to 'normal' until about July 1974. Some of this prolonged effect must have been directly due to the flood, in terms of continued drainage from the surrounding country and in terms of slow dissipation. A second period of higher than usual rainfall in March 1974 accompanying a cyclone is believed to have played an important part in prolonging the period of reduced salinity.

The flood produced early effects on the sediments of the area, and caused a 'blanketing' of the surface by a layer of soft mud several cm thick. It is unfortunate that pressure of work precluded adequate investigation of this phenomenon. Its

very existence suggests that while the earliest flood effects would involve dilution, before a month had elapsed both dilution and siltation would be involved.

Fourteen months after the flood there was evidence of a 'permanent' change in the sediments of the area, with an overall increase in the muddiness, and a complex pattern of sediment distribution of the eastern side of the sampled area, nearest to the Brisbane R.

One of the biotic effects which became detectable in late postflood was an increase in the population (of all species summated) in the area as a whole. It is tempting to relate this to the increased muddiness, and hence increased supply of mud-associated nutriment, to the area. The main species involved in the population increase was *Spisula*, which in our preflood investigations was not associated with the muddier grounds, but which is known to occupy muddy areas within the estuary of the Brisbane R. (Hailstone 1972). Whether, with the muddiness remaining in the area, populations will remain high is uncertain (see below).

COMPARISON WITH THE LITERATURE OF FLOOD EFFECTS ON BENTHOS: While there have been several autecological and physiological reviews of the effects of sudden dilution on benthid organisms (e.g. Pearse and Gunter 1957, Gunter *et al* 1973) the literature on 'community' effects does not appear to have been consolidated and the present account is likely to be incomplete.

Most of the Queensland literature has been concerned with the effects of dilution and sediment suspension upon coral biotas. It includes Hedley (1925), Rainford (1925), Fairbridge and Teichert (1947, 1948), Stephenson (1956), Endean, Kenny and Stephenson (1956), Stephenson, Endean and Bennett (1958), Slack Smith (1960), and Lovell (1976). In general there is slow recovery from flood damage, in some cases taking years and in other cases it is doubtful if recovery to the preflood situation will ever occur (Rainford 1925). It appears that where flooding occurs only at very infrequent intervals a complex biota of species which lack flood tolerance develops, and that this takes a long period to redevelop after a flood. An interesting example of coral effects was reported by Hedley (1925) and apparently has generally been overlooked in the literature. It involved a layer of freshwater floating for several days on the surface of the sea, and a probability that putrefaction and deoxygenation contributed to the devastation.

Studies involving a mixture of hard-bottom epibiota, soft-bottom epibiota and soft-bottom infauna have been carried out by Fischer-Piette (1931) in France, MacGinitie (1939) in Southern

California, Sandison and Hill (1959) in Lagos, and Goodbody (1961) in Jamaica. In each case the hard-bottom epibiota was the most affected, especially the tunicates. MacGinitie (1939) suspected that most of the soft-bottom biota, especially the infauna, escaped the effects of the brief dilution he considered.

The floods described in the literature involve different periodicities, different degrees of salinity reduction and of putrefaction and also different durations. Regular annual flooding occurs at Lagos in East Africa (Hill and Webb 1958) and the original biota returns in 1–2 months without any succession (Sandison and Hill 1959). In Queensland there is something approaching a wet summer season but this occurs irregularly and the present floods lie somewhere between the augmentation of a normal seasonal flood as described by Fischer-Piette (1931) and by Goodbody (1961) and the very occasional catastrophe described by MacGinitie (1939).

In several of the literature cases, as with Hedley (1925), a distinct layer of freshwater remained on the surface after flooding, and the biotic effects were virtually restricted to the shallower organisms (MacGinitie 1939, Sandison and Hill 1959 and Goodbody 1961). In the present case the entire area was affected, involving depths to 5 m and no doubt beyond. It is true that the deepest water furthest from the Brisbane R. was somewhat less affected than the remainder.

The duration of flood effects as reported in the literature ranges from a matter of days (MacGinitie 1939) to more than a month (Goodbody 1961). Goodbody noticed that prolonged dilution of Kingston Harbour, Jamaica caused the greatest effect, and in the present case it appears that the duration of dilution has been a major factor contributing to the biotic effects.

Flood recolonisation does not appear to have been closely studied. Goodbody (1961) described recolonisation as starting after two months, and this would agree with our observations. MacGinitie (1939) noted that recolonisation was complete after nine months but added that many species had by then established themselves in larger numbers than were present before the flood. This 'over-response' has only applied to a limited number of species in the present data, and specifically to the bivalve *Spisula*. MacGinitie (1939) considered the over-response as being due to a deposition of sediment improving the food supply. This could apply in the case of *Spisula*, but additional factors could well include an elimination of competitors and reduction of predation levels. The present data suggest that the immediate effect

of sediment deposition might have been harmful to the biota.

None of the overseas surveys, apart from that of Stone and Reisch (1965) considered numerical data, and their study involved only three species. The only past study involving numerical data on many species appears to be that of Stephenson, Williams and Cook (1974) at Peel Island in Moreton Bay. During the Peel Island study a flood occurred and this by present standards would be described as 'minor'. Flood effects were postulated to cause an overall increase in complexity and the authors stated (p. 110): 'gross instability is likely to lead to reduction in complexity, whereas instability within acceptable limits may well increase it'. The present floods are an example of the former.

POSSIBLE LONG TERM CHANGES: Flood data summarised by Ward (1974) show that the 1974 flood was not, by hydrographic standards, the most severe one which has affected the Brisbane R. since records have been kept. The worst recorded floods were in the 1840's followed by two severe floods in the 1890's and then by the 1974 flood. In addition there have been concentrations of floods of somewhat lesser intensity roughly 25 years ago, and roughly 50 years ago.

We now make two assumptions. The first is that floods will affect the biota of Bramble Bay at roughly 25 year intervals. The second is that effects will be roughly comparable with those described for the 1974 flood. On these bases within about a year of the flooding there will be recovery to the point of Bramble Bay being occupied by a *Spisula-Parcanassa* community with high populations but low diversity. At this stage there will also be a recovering offshore population in which *Paratapes* will be dominant, accompanied by ophiuroids. This offshore population will be more diverse than that over the remainder of the area.

As time proceeds one would expect the area of dominance of *Spisula* to decrease. One likely cause of this restriction will be predation by the gastropod *Parcanassa* whose populations about a year after the flood were roughly double those before the flood. It is possible that there will be 'Gaussian' oscillations in the populations of these two species with predator overeating its food supply and hence declining, and with resultant secondary increases in *Spisula*. Oscillations of this nature could well explain some of the chronological changes in the biota in the preflood period as investigated by Stephenson, Raphael and Cook (1976).

The long term rate of recovery to a broad *Spisula-Anadara-Paratapes* situation is not known

except that presumably it takes less than 25 years. Equally unknown is whether the chronological changes at such a time are oscillations about a state of pseudo-equilibrium triggered by environmental changes (e.g. annual wet season) or whether they are progressive stages towards a climax situation which was still not attained in 1973.

It is clear that further investigations of the area are required and these are in train. It is equally clear that any detailed predictions of the effects of enlargement of Brisbane Airport should be linked to a given stage of recovery from flood effects. It is suggested that the effects of airport enlargement are likely to be much less obvious than those caused by the natural 'catastrophes' of early 1974.

ACKNOWLEDGMENTS

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APPENDIX

Code numbers and species in order of abundance in preflood samples ($27 \times 7 + 21 \times 2$); only species occurring > 11 times listed. For systematic groups see Stephenson Raphael and Cook 1976, pp. 445–6.

1	<i>Spisula trigonella</i> (Lamarck)	38	balanid 1
2	<i>Mesochaetopterus minutus</i> Potts	39	<i>Edwardsia</i> sp.
3	<i>Xenophthalmus pinnotheroides</i> White	40	<i>Onuphis</i> sp.
4	<i>Paratapes scordalus</i> Iredale	41	<i>Placamen sydneyense</i> Menke
5	<i>Anadara trapezia</i> Deshayes	42	<i>Dasybranchus caducus</i> (Grube)*
6	<i>Amphioplus</i> sp.	43	<i>Arca</i> sp. 1
7	<i>Amphioplus lobatus</i> (Ljungman)	44	oyster 3
8	<i>Theora lata</i> Hinds	45	<i>Amphioplus depressus</i> Ljungman
9	<i>Terebellides stroemi</i> Sars	46	<i>Trichomya hirsuta</i> (Lamarck)
10	<i>Amphitrite rubra</i> (Risso)	47	<i>Leptomya pura</i> Angus
11	<i>Pupa fumata</i> (Reeve)	48	<i>Mesochaetopterus</i> sp.
12	<i>Theora</i> sp.	49	aphroditid 1
13	<i>Amphipholis loripes</i> Koehler	50	<i>Leonnates stephensoni</i> Rullier
14	<i>Leanira yhleni</i> Malmgren	51	<i>Clorida granti</i> (Stephenson)
15	<i>Parcanassa mangeloides</i> Reeve	52	<i>Marphysa sanguinea</i> (Montague)
16	<i>Lumbrineris latreille</i> Audouin and Milne Edwards	53	<i>Glossobalanus hedleyi</i> Hill
17	<i>Loimia medusa</i> (Savigny)	54	<i>Reticunassa paupera</i> Gould
18	tunicate 1	55	nemertean 'pink'
19	tunicate 3	56	whip coral
20	bivalve 1	57	<i>Venus</i> sp.
21	<i>Nucula astricta</i> Iredale	58	<i>Macoma donaciformis</i> Deshayes
22	oyster 1	59	<i>Ophiactis perplexa</i> Koehler
23	<i>Pectinaria antipoda</i> Schmarda	60	<i>Anomia</i> sp.
24	<i>Nereis jacksoni</i> Kinberg	61	amphipod 4
25	<i>Mesochaetopterus capensis</i> (McIntosh)	62	<i>Elamenopsis lineata</i> A. Milne Edwards
26	<i>Ophelina gigantea</i> Rullier	63	<i>Pista</i> sp.
27	sea anemone 1	64	amphipod 2
28	<i>Isolda pulchella</i> Müller	65	<i>Amaeana trilobata</i> (Sars)*
29	bivalve 2	66	<i>Hexapus granuliferus</i> Campbell and Stephenson
30	<i>Tellina texturata</i> Sowerby	67	tunicate 2
31	<i>Glycera prashadi</i> Fauvel	68	<i>Chaetopterus variopedatus</i> Renier
32	<i>Cirriformia</i> sp.	69	Sabellid 1
33	<i>Protankyra</i> sp.	70	<i>Natica</i> sp.
34	<i>Petaloproctus terricola</i> Quatrefages*	71	amphipod 6
35	bivalve 3	72	<i>Tapes watlingi</i> Iredale
36	<i>Chama fibula</i> Reeve	73	amphipod 1
37	<i>Cycladicama</i> sp.	74	<i>Bedeia hanleyi</i> Angus

*Possibly misidentified.

PENAROSA NETENTA, A NEW MIDDLE CAMBRIAN TRILOBITE
FROM NORTHWESTERN QUEENSLAND

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ABSTRACT

A new species, *P. netenta*, is described and assigned to the nepeid genus *Penarosa* Öpik, 1970. The pygidium of *Penarosa* is correctly identified from this new species and, as the same pygidial type is known to occur in *Nepea*, it is taken to be typical of the family.

The only previous knowledge of the Nepeidae comprises the original description of *Nepea narinosa* Whitehouse, 1939, with a considerable discussion of its possible relationships (Whitehouse 1939, pp. 210–11); a reinterpretation of *N. narinosa* with clarification of all cephalic structures (Öpik 1963); description of two Upper Cambrian genera (Öpik 1967); and a monograph of Middle Cambrian species in 4 genera (Öpik 1970). This paper proposes a new specific name, provides a detailed description in modern terms of every aspect of the morphology of a nepeid species, and correctly identifies its pygidium pointing out Öpik's (1970) probable error in assignment of a pygidium to *Penarosa retifera* Öpik, 1970.

The material is deposited and catalogued (QM) in the Queensland Museum, Brisbane.

I am thankful to Dr J. B. Jago, South Australian Institute of Technology, Adelaide, for providing me with a latex cast of an uncatalogued, undescribed species of *Nepea* from Tasmania.

Family NEPEIDAE Whitehouse, 1939

Genus *Penarosa* Öpik, 1970

Penarosa Öpik, 1970, p. 24. (*Type species: P. retifera* Öpik, 1970, p. 25, figs. 9–10, pl. 8, figs. 1, 2; pl. 9, figs. 1, 2, 4; pl. 17, figs. 7–9 from the Age Creek Formation and Current Bush Limestone, north-western Queensland and Northern Territory, *Euagnostus opimus* Zone, late Middle Cambrian; by original designation.)

Trinepea Palmer and Gatehouse, 1972, p. 25. (*Type species: T. trinodus* Palmer and Gatehouse, 1972, p. 25, pl. 4, figs. 1, 2 from the Nelson Limestone in the Neptune Range, Antarctica, *Amphoton oatesi* faunule, late Middle Cambrian; by original designation.)

DIAGNOSIS: Öpik's (1970, p. 24) diagnosis of the genus stands.

REMARKS: When Palmer and Gatehouse (1972) described *Trinepea*, they did not refer to Öpik's paper in which *Penarosa* was described. The size of the three bosses on the brim, the unpaired ocular ridges and the short (sag.) anterior border furrow are the only characters quoted as distinguishing *Trinepea*. In fact the lateral bosses on the brim are of similar size to those of several species of *Penarosa* (cf. Öpik 1970, pl. 9, fig. 5a; pl. 12, fig. 2b; pl. 13, fig. 1b); in several specimens figured by Öpik the ocular ridges are not clearly bifurcate (1970, pl. 9, fig. 1; pl. 12, fig. 2a) and in others the bifurcation only appears distally, a position where Palmer and Gatehouse's single figured specimen is damaged; and the short border furrow is only of specific value. *Trinepea* is thus clearly synonymous with *Penarosa*.

Penarosa netenta sp. nov.

Figure 1; Plate 21, figs. 1–8

Etymology: An anagram from my wife's name—Annette.
MATERIAL EXAMINED

HOLOTYPE: QMF7059, a cranidium from locality QML152.

PARATYPES: QMF7060–70, a cranidium, two free cheeks, an incomplete thorax and a thorax plus pygidium from locality QML152; and four cranidia and two free cheeks from locality QML136.

Queensland Museum locality L152 is 1.7 km south of Chummy Bore which is 6 km west of Thornton Homestead on the road to Camooweal at 19°31.5'S., 138°52'E. and QML136 is at Chummy Bore. The material occurs in weathered red, white or yellow siliceous shales of the Chummy Bore Formation (De Keyser and

Cook 1972) exposed in the low ridges just south of Chummy Bore as far as QML152. The associated agnostoid trilobites indicate an age within the Zone of *Euagnostus opimus*.

DIAGNOSIS: Member of *Penarosa* with upturned, slightly concave anterior border and border furrow; poorly vaulted cranium; reticulate caeca of the respiratory prosopon (Jell, in press) on the brim but not in the border furrow; no transverse ridge on the brim; preglabellar boss as wide as the glabellar anterior and reaching the anterior border furrow in most specimens; 3 pairs of lateral glabellar furrows; ornament of coarse tubercles and finer interspersed granules; large distally expanded posterolateral limbs; more than 25 thoracic segments; an extremely small, simple, almost flat, transverse pygidium with an indistinct slightly elevated axis.

DESCRIPTION: Semicircular cephalon 0.5–0.6 times as long as wide. Glabella moderately convex, but remainder of cephalon relatively flat except for the posterior limbs. Comparatively short glabella (0.75 of preglabellar length) very slightly tapering anteriorly, with a squared anterior margin, more conspicuous by prominent, square, to slightly

expanded, anterolateral corners. Occipital ring longest and relatively flat sagittally with a short almost vertical posteromedial spine; its posterior margin straight (tr.) over axial two-thirds but slightly anteriorly curved distally to the axial furrow. Occipital furrow well impressed laterally but shallow over the axial two-thirds, running posteriorly up from the axial furrow for slightly less than 0.25 of glabellar width, then anteriorly to meet the sagittal line at 70° to 80° . Other glabellar furrows discontinuous axially. Furrow 1p best impressed, directed posteriorly at 45° to axial furrow and, from internal moulds, apparently forked adaxially. Furrow 2p parallel to furrow 1p, but furrow 3p directed anteriorly at 45° to axial furrow. Axial furrow very deep, uniform width, steeply walled against the glabella but with more gently inclined abaxial wall; accommodating small low bacculae adjacent to lobe 1p, and crossed anteriorly by the strong eye ridge.

Preglabellar furrow moderately deep with rounded section (sag.), lateral fossulae just in front of eye ridges only slightly deeper than the rest of the furrow and with slightly steeper posterior wall than anterior one. Median boss dominant on the brim, equal in width (at its widest point) to glabellar anterior, tapering slightly forward, extending from preglabellar to border furrow, highest 0.3 of its length from the posterior from which point it descends very gently anteriorly and is bounded laterally by broad, very shallow, parallel furrows running from fossulae to border furrow. Lateral brim areas rising very gently from these furrows not inflated. Long (sag.) shallow border furrow with rounded bottom leading anteriorly to a short, flat to slightly concave, upturned, narrow (tr.) (by comparison with other species of the genus) anterior border. Anterior doublure long (i.e. half the border length) near the axis but soon tapering to almost nothing laterally. Shortly after crossing the margin the facial suture curved posteriorly to a sharp corner then as the rostral suture directly across the axis. Rostral plate unknown but, by fitting the free cheek with this anterior doublure, clearly defined.

Prominent eye ridges bifurcate near the axial furrow, then as two contiguous ridges in a straight to slightly anteriorly convex arc to the palpebral lobe anterior. Palpebral lobe not bifurcate (as the eye ridge), kidney shaped with the adaxial extremities in an exsagittal line and δ (at its widest point) behind its midlength; a raised ridge parallel and close to its abaxial margin; from this ridge sloping gently and flatly into a narrow, poorly impressed, palpebral furrow. Palpebral furrow turning abaxially behind the palpebral lobe. Fixed cheek width

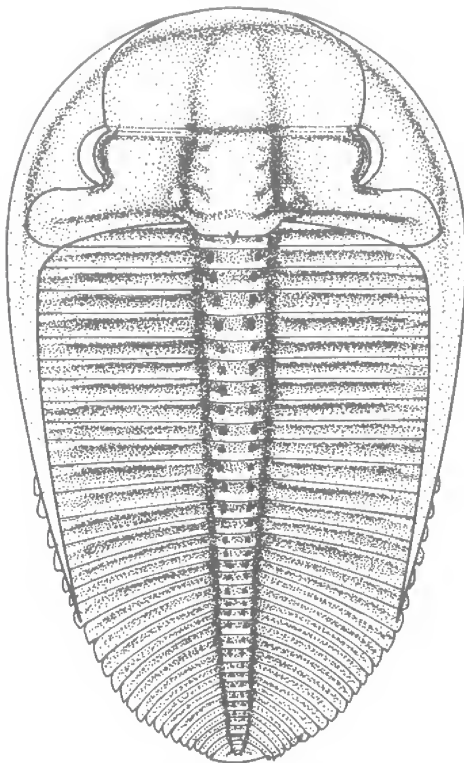


FIG. 1: Reconstruction of *Penarosa netenta* sp. nov. drawn from Plate 21, figs. 2, 3a and 6.

1.3 times basal glabellar width. Facial suture opisthoparian, suture crossing border and border furrow very obliquely. ζ - ζ is narrow. β near the midlength (exsag.) of the brim and only just abaxial to ζ giving the anterior branch an anterolaterally convex shape. ε opposite the midpoint of the glabella. Posterior margin straight (tr.) to the fulcrum then curved markedly posteroventrally to ω and just beyond before straightening slightly on the genal spine. Short posterior border convex adaxially but lengthening and flattening beyond the fulcrum. Posterior border furrow short and moderately deep adaxially, deepening adjacent to the fulcrum, then ceasing to be a discrete furrow; abaxially a very shallow broad depression as far as the facial suture. Posterior limb enlarged laterally, swinging posteriorly as a rather flat lobate structure. Posterior branch of the facial suture transverse from ε for a short distance then curved posteriorly and finally swinging around the ovate to round termination of the posterior limb to the posterior margin. Posterior border and occipital ring not connected, instead occipital ring dying out into the posterior border furrow and lobe 1p connected through the baccula to the postero-proximal corner of the fixed cheek.

Ornament on the exoskeleton varying from one area to another; absent on the smooth palpebral lobes and in the axial furrow, whereas on the fixed cheeks and central boss a single order of moderately large, relatively sparsely scattered tubercles present. On the remainder of the cranidial exoskeleton, a much denser ornament of moderately sized tubercles and interspersed granules an order of magnitude less than the tubercles evident. The brim exhibiting a respiratory prosopon of generally parallel sometimes anastomosing ridges running forward from the eye ridges and preglabellar furrow to the border furrow. The majority of the large brim tubercles appear to be on the caecal ridges.

Free cheek dominated by the genal spine but also with a trapezoidal subocular part and a posterior part extending back into the genal spine. Subocular part with strongly upturned though uniformly low eye socle, with gently abaxial slope anteriorly becoming much steeper posteriorly, with shallow narrow, moderately distinct border furrow, flat only slightly upturned border and typical cephalic brim prosopon. Large embayment in the free cheek, accommodating the posterior cranidial limb; extending to the border furrow. Small posterior part sloping steeply abaxially; crossed by a shallow border furrow fading out on the genal spine; with a sharp point adaxially on the posterior margin and drawn out posteriorly into a strong

genal spine extending posteriorly at least to within 15 segments length of the pygidium and possibly further.

Doublure extending only to the border furrow in the subocular area; rounded section (tr.) leaving a large volume between it and the dorsal border; anteriorly very close to the dorsal surface marginally, well separated from the dorsal exoskeleton at the border furrow and returning to just beneath the brim for a short distance posteriorly; sutural ending adaxially as described above; inner margin curved adaxially across the base of the genal spine to the posterior margin where doublure virtually absent. Genal spine with complete doublure (i.e. hollow) and shallow ventral medial furrow fading out posteriorly. Doublure with a uniformly tuberculate ornament throughout.

Thorax of 25 or more segments but probably not more than 35. Anterior thoracic width slightly less than cranidial width as posterior limbs extend beyond pleural tips. Width constant to midlength (exsag.) but tapering strongly beyond this point. Genal spines curved in, to be touching pleural tips from mid to three quarter length. Segment shape varying through the thorax from directly transverse (between the fulcra) anteriorly to markedly anteriorly convex near the posterior (last 10–15 segments). Axial to pleural width ratio decreasing posteriorly from 0.56 for first 10 segments down to 0.4 in front of pygidium. Short half ring equal in length to the articulating lobe and maintaining its length almost to the axial furrow where it tapers sharply to nothing. Articulating furrow well impressed, shallowest at axial furrow then deepest and longest a third of the way to the sagittal line; with steep almost vertical anterior wall to the angular posterior margin of the half ring and more gently sloping posterior wall; with lateral pits representing apodemes (even more prominent on internal moulds extending almost to the level of the floor of the axial furrow and being slightly expanded adaxially as well as extending to the axial furrow). Articulating lobe expended just abaxial to the apodemal pits; bearing ornament of tubercles slightly finer than the cephalic ones. Pleural furrow dominating the pleura by occupying its entire length adjacent to the axial furrow and at least three quarters of the length as far as the fulcrum; beyond this point shallowing and shortening to finish near rounded pleural tips; anterior wall is almost vertical and posterior wall, although steep (to 60°) adaxially is more gently sloping. Extremely short (exsag.) pleural bands of variable but generally equal length, increasing gradually in length beyond the fulcrum, coalescing near the pleural tip and carrying a single prominent row of fine

tubercles. Wide (tr.), short (exsag.) poorly defined facet present anterolaterally. The prominently convex axis stands above the pleural areas that are deflexed ventrally in the fulcral line.

Pygidium extremely small, almost oval with curved anterior margin against the last thoracic segment and curved posterior margin rounding off the posterior of the exoskeleton. Axis occupying more than half width; reaching almost to the posterior margin; slightly raised above pleural areas; and with at least 2 very poorly impressed transaxial furrows. No axial furrow. Articulating half ring not preserved on this specimen. Pleural areas smooth.

Intraspecific variation is restricted to slight variability in size and shape of the palpebral lobe, size of the posterior limb, upturning of the anterior border, and ornament.

REMARKS: The material is preserved in a porous siliceous shale so that the 'furry' appearance of the latex casts is partly the result of the latex having penetrated the minute pores of the matrix. Several specimens have been crushed by compaction but the breakages are obvious. Uncrushed specimens definitely have a low cephalic convexity. On the specimen figured in Plate 21, fig. 6, there are grooves along the pleural tips with tuberculate ornament in the bottom. These are interpreted as the external moulds of genal spines, and the specimen is thought to be a damaged fragment of one originally fossilized with its entire dorsal exoskeleton in place.

Öpik (1970, p. 28, text-fig. 11, pl. 9, fig. 3) described a pygidium with four axial rings, longer than half its width, and with a row of pustules on each pleural band, as belonging to *Penarosa retifera*. This pygidium, estimated by Öpik to be 0.2 to 0.25 of cephalic length, would be relatively large for the thoracic segments of *P. retifera*. It is not associated with any thorax or cephalon. The pygidium described for *P. netenta* below (Plate 21, fig. 6) is very much smaller, being less than 0.1 of cephalic length and only slightly wider than long. It is associated with a thorax the anterior segments of which exactly match those associated with the cephalon of *P. netenta*. Further, the associated thorax bears laterally a groove with rounded pitted floor that exactly matches the position, shape and ornament of the genal spine of a penarosid. From these observations it can definitely be concluded that the pygidium belongs to a species of *Penarosa*, namely *netenta*, the associated cephalic specimens. Moreover, the pygidium of a poorly preserved but complete specimen of an undescribed nepeid species from the Christmas Hills, northwestern Tasmania, is almost identical with that described in

P. netenta below. No such conclusion can be reached about Öpik's identification of the pygidium of the very closely related *P. retifera*. On the contrary there are good reasons for believing that his identification is not correct and that the pygidium he assigned to *P. retifera* does not belong to the Nepeidae at all. Thoraxes of *Nepea* and *P. netenta* show a progressive reduction of the pustules on successive segments, and that they are absent on the most posterior ones and on the pygidium. Öpik's specimen exhibits pustules very much larger than those on the associated cephalon. Moreover, judging from the sizes of the known pygidia of *Nepea* and *P. netenta*, the total width of the pygidium is only about half the width of the occipital ring of the same individual, whereas the proposed pygidium of *P. retifera* would be at least equal to the occipital width of the same individual. Differences of this magnitude are unlikely in view of the conservative nature of the pygidium throughout a wide range of related genera. For example the related species *Alokistocare harrisi* Robison, 1971 and *Bolaspidella wellsvillensis* (Lochman and Denson, 1944) figured by Robison (1971, pl. 91) show remarkable pygidial similarity to *P. netenta* and *Nepea* sp. nov.

Öpik described and figured (1970, p. 39, pl. 16, fig. 2) the free cheek unit of *Penarosa petalifera* and concluded that no median suture or rostral plate existed. The ventral structure of *P. netenta* is somewhat different. The sutures described on the doublure (Pl. 21, fig. 7) along with the appearance of a sutural termination to the anterior of the free cheek (Pl. 21, fig. 5) indicate clearly the presence of connective sutures and a rostral plate, very much like that described for species of *Bolaspidella* (Robison 1964, pl. 88, fig. 19) and indeed structurally similar to most ptychoparioid rostral plates. The suggestion is made that Öpik's specimen, if prepared further may turn out to be a complete animal that has not moulted. If this is not the case then fusion of the sutures has occurred in this youngest species of the lineage.

Of Öpik's (1970, p. 45) three groups within *Penarosa* this new species belongs to the 'rimless' *retifera* and *vittata* group which also includes his sp. nov. PC, sp. nov. PD and sp. nov. PE. *Penarosa vittata* is distinguished by the transverse ridge in the anterior border furrow, much wider fixed cheeks, smaller posterior limb, narrower median boss, better impressed glabellar furrows and more prominent venulose brim ornament. *Penarosa* sp. nov. PD and sp. nov. PE are not sufficiently preserved for comparison. *Penarosa retifera* is distinguished by its highly vaulted cephalon, its fourth lateral glabellar furrow, narrower median boss, more

tapering glabella, wider fixed cheeks, denser fixed cheek ornament, more anteriorly expanded posterior limb, and venulose ornament extending through the border furrow on to the border. *Penarosa* sp. nov. PC is probably conspecific with *P. netenta* but the figured specimens do not allow complete agreement to be reached. Öpik's text-fig. 14 appears to show a fourth lateral glabellar furrow, a narrow boss (damaged) and wide, convex, palpebral lobe.

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PLATE 21

Penarosa netenta sp. nov.

All figures are dorsal views of internal moulds unless otherwise stated.

FIG. 1: Holotype cranidium QMF7059, $\times 4$; b, latex cast, with 'furry' texture of the latex well shown on the smooth agnostoid pygidium in the lower left.

FIG. 2: Oblique lateral view of damaged right free cheek showing the respiratory prosopon on the subocular area and the mould of the tuberculate doublural ornament extending down the genal spine QMF7068, $\times 6$.

FIG. 3: Cranidium with fifteen thoracic segments attached showing the prosopon on the brim, the double eye lines and overlap of posterolateral limb on the thorax QMF7065, $\times 5$; b, oblique lateral view showing the upturned border and slightly enrolled thorax.

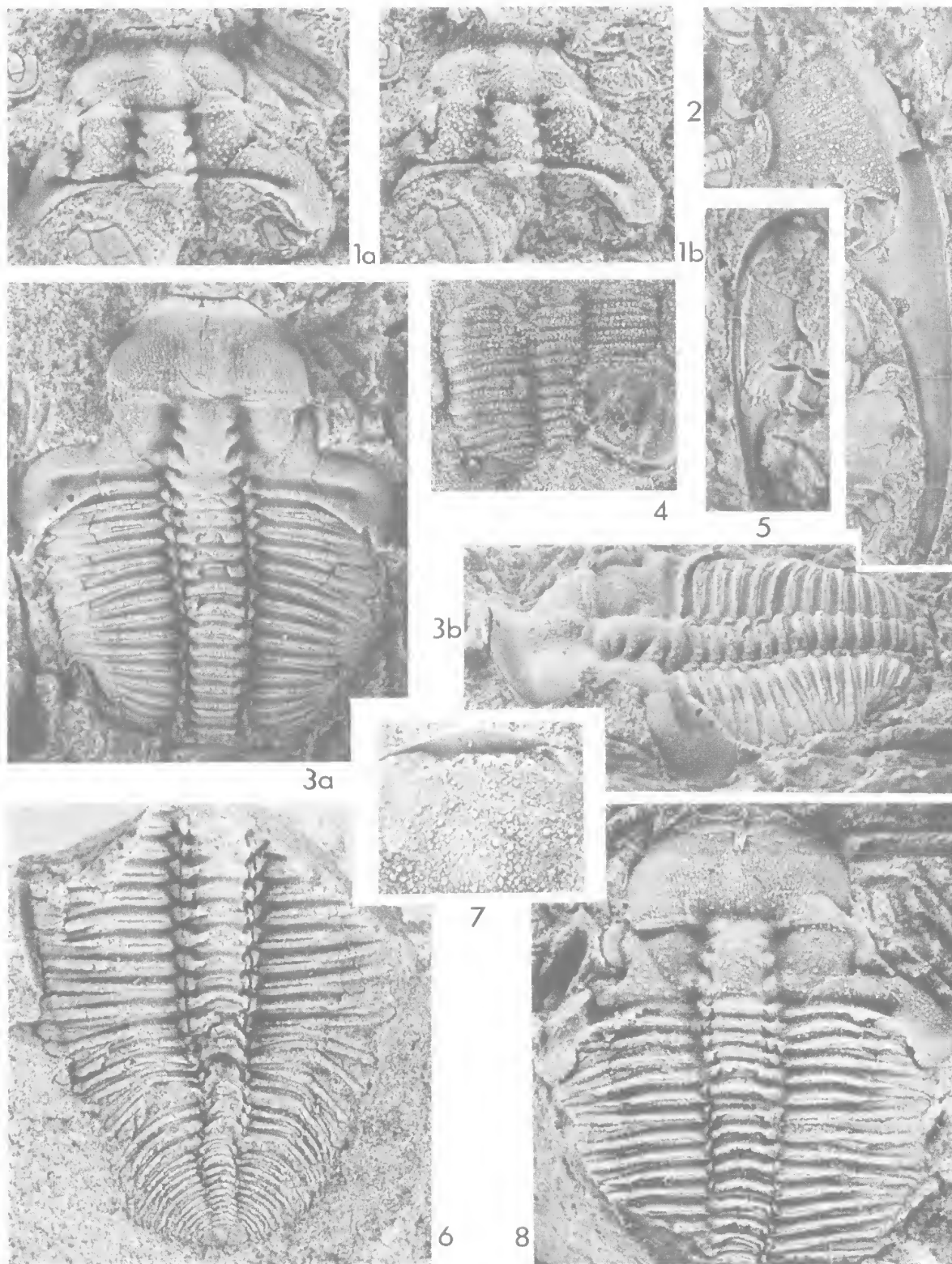
FIG. 4: Latex cast of thoracic fragment showing the single row of pleural tubercles on each pleuron QMF7064, $\times 5$.

FIG. 5: Oblique lateral view of left free cheek showing the doublure extending adaxially beyond the border furrow anteriorly, the convexity of the doublure and the mould of the furrow on the genal spine QMF7060, $\times 4$.

FIG. 6: Damaged thoracic fragment of 25+ segments with pygidium attached showing the moulds of the genal spines laterally QMF7062, $\times 5$.

FIG. 7: Anterior of cranidium showing the cephalic doublure and the course of the facial sutures and rostral suture QMF7069, $\times 6$.

FIG. 8: Cranidium with 14 thoracic segments attached QMF7061, $\times 5$.





OBITUARY

Thomas Claude Marshall
1896–1976

Tom Marshall was born in Brisbane 2nd January, 1896 and died in his home city on 30th June, 1976. Although the latter part of his career was in the Fisheries Section, Department of Harbours and Marine, he was for 32 years, an enthusiastic staff member of the Queensland Museum. He contributed a great deal during a period of staff shortages and difficulties of many kinds.

He joined the Queensland Museum in 1910 and even at this age had a small collection of insects, fish and birds. This early interest in Natural History developed into a life work, culminating in his study of the Great Barrier Reef and Queensland fishes.

On 15th January, 1912, Tom Marshall was appointed as a Cadet. Under the influence of Anthony Alder, he soon learnt to produce excellent casts of fish and other natural history specimens and to paint them in life-like colours. Many of the scores of specimens he prepared are still on display in the fish gallery of the Queensland Museum.

After World War I, in which Marshall served with the 13th Australian General Hospital Unit, he continued his work at the Queensland Museum and became closely associated with the Ichthyologist, James Douglas Ogilby. This association fired his enthusiasm for the collection, classification and nomenclature of Queensland fishes, an enthusiasm that was shared with his friend George Coates, of Townsville, who collected and donated to the Queensland Museum many hundreds of fish specimens. Coates painted excellent water-colours of tropical fish, many of which were later published by Marshall, and he was undoubtedly a major influence as Marshall developed his own expertise in the preparation of coloured sketches of fish as an aid in identification and for the painting of casts.

In the mid 1920's Tom Marshall founded the 'Aquarium and Terrarium Society of Queensland' and was the society's first President. At about this stage he made a study of Conchology and derived much pleasure from his shell collection until the end of his life.

By the late 1930's his interest turned to film making. His two colour films, 'Enchanted Regions of the Great Barrier Reef', 1939, and 'Roving Coral Seas', 1940, were very successful and were widely shown throughout Queensland and interstate.

These films aroused public interest in the animals of the reefs and the beauty of the coral cays and islands. Considerable help and encouragement was provided for Tom Marshall at this time by the Director of the Queensland Museum, Mr Heber A. Longman.

He collected widely on his many trips to the islands of the Great Barrier Reef. In 1938, with E. G. Ogg, an Honorary Collector, he collected fish specimens at Prince of Wales and Yorke Islands in the Torres Straits and during October–November of the same year, Marshall collected and surveyed the fishes of the Barcoo and Thompson Rivers of Western Queensland.

Marshall was appointed Artificer and Modeller on 1st July, 1925 and he held this position for nearly 17 years even though much of his work was research on Queensland fishes.

In 1939, he was awarded a Carnegie Scholarship to study abroad but this was held over due to World War II, and afterwards, because of his age, he was precluded from proceeding with the scholarship.

On the 6th March, 1942, he was seconded to the Fisheries Section, Department of Harbours and Marine and on the 6th May, 1943 was appointed Assistant Chief Inspector of Fisheries. Nearly three years later, now Ichthyologist, he was in charge of the scientific studies in his department, the position he held until his retirement in 1962. For many years, and until the time of his death, Marshall was a member of the Great Barrier Reef Committee. His enthusiasm for the Queensland Museum never waned, and he took great pleasure in the new displays for he had always had a flair for this side of museology.

His papers on various ichthyological subjects were published in the *Memoirs of the Queensland Museum*, and in *Ichthyological Notes of the Department of Harbours and Marine*. His *magnum opus*, 'Fishes of the Great Barrier Reef and the Coastal Waters of Queensland' appeared after his retirement in 1964 and remains to the present, a valuable textbook for the scientist and layman alike. George Coates' beautiful plates of fishes are printed in this work.

Tom Marshall was a friendly man of out-going personality with a repertoire of humorous stories and anecdotes of earlier days at the Queensland Museum.

Behind most important men there is often an inspiring woman, and in Marshall's life it was his wife, Dot. Formerly Dorothea Agnes O'Donnell, she contributed very considerably in providing a happy home in which they reared one son and three

daughters. On the innumerable occasions when interstate and international scientists and Ichthyologists were invited to his home at Eagle Junction she was an untiring hostess. To his wife Dorothea, his son Walter and his daughters Thelma, Gwen and Audrey we extend our sincere sympathy.

D. P. VERNON.
Queensland Museum



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